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A COMPARISON OF THE VARYING SALINITY CONDITIONS OF THE TEES AND SEVERN ESTUARIES*

BY R. BASSINDALE, *Department of Zoology, Bristol University*

(With 1 Map and 8 Figures in the Text)

1. INTRODUCTION

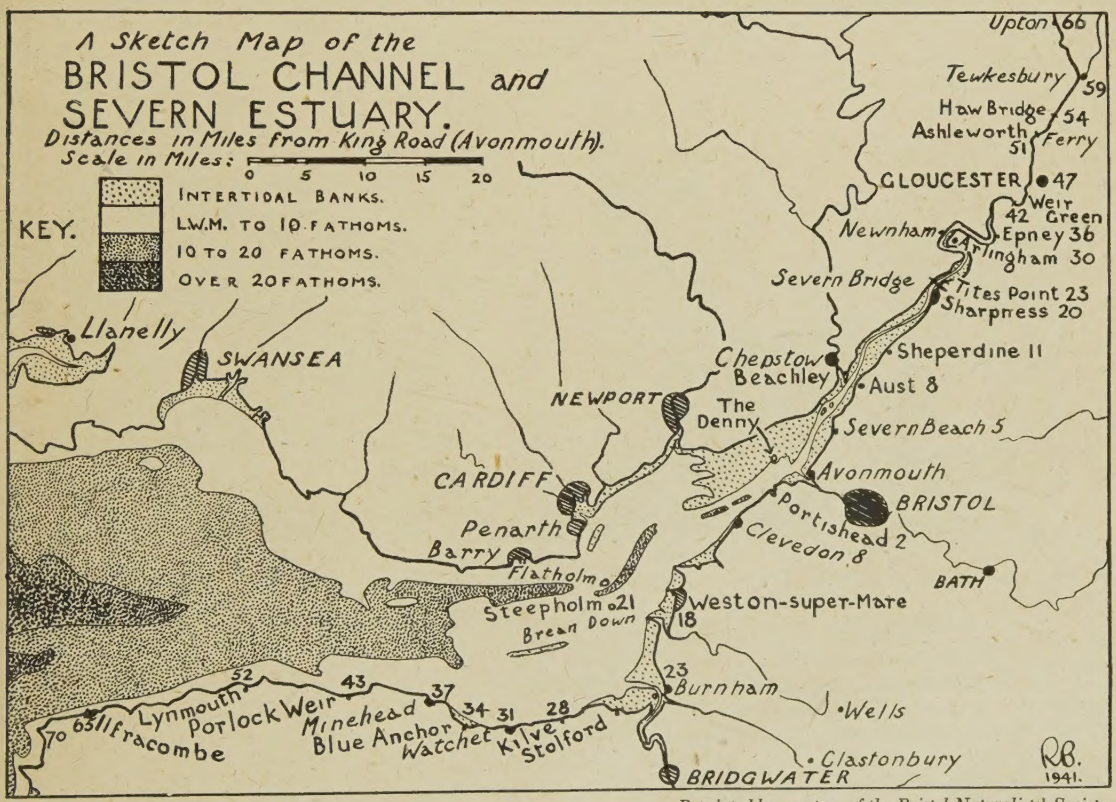
Recent investigations have been made into the variations of physical conditions in estuaries, but attention has been directed neither to the presentation of a detailed estimate of the variations to which animals in different regions are subjected nor to a comparison of estuaries of different types. The present account attempts both these objects and is based mainly on work carried out by the Admiralty on the Severn and Tees (Gibson, 1933; Denman, 1931) supplemented by observations on the Severn by the present author (1943) and on the Tees by the Water Pollution Research Board (Alexander, Southgate & Bassindale, 1935).

* No. 11 of a series on the Biology of the Bristol Channel.

2. THE SEVERN ESTUARY

(a) *Tides and salinity*

The tidal regime of the Severn is exceptional because of the extreme range of tide. The following points are taken from a fuller account (1943) and illustrated in Fig. 1B of Bassindale (1942):



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(1) The tide wave which affects the Bristol Channel at Swansea sweeps up the Channel and estuary with an increasing amplitude until at Aust the rising bed of the river cuts off the lower part of the wave and so gradually reduces the range of tide so that at Upton-on-Severn only the largest tide is experienced.

(2) Owing to the elimination of the lower part of the tide wave and to the increased friction produced

by the rising bed of the estuary the foot of the tide wave is increasingly retarded so that the flood tide takes less and less time as the estuary is ascended. In addition, part of the wave front becomes vertical during spring tides as the bore wave which disturbs the estuary from below Arlingham to Gloucester.

(3) The large amount of water forced up the narrow reaches by the largest spring tides has not sufficient time to drain away during the ebb. This causes all places above Sharpness to have a lower low water on neaps than on springs. This is the reverse of conditions below Sharpness and on the open sea coast.

(4) At any given time and place the water is of the same salinity at all depths, i.e. there is no vertical salinity gradient.

(5) Salt water penetrates the estuary much farther during summer than during winter and during spring tides than during neaps.

(6) Summer neap-tide salinities are higher than winter spring-tide salinities.

(7) Salt water penetrates on spring tides beyond the limit of action of neap tides, so that the reaches about Epney are not tidal during neap tides but may be subject to high salinities at high water of spring tides and to medium or low salinities at the corresponding low waters.

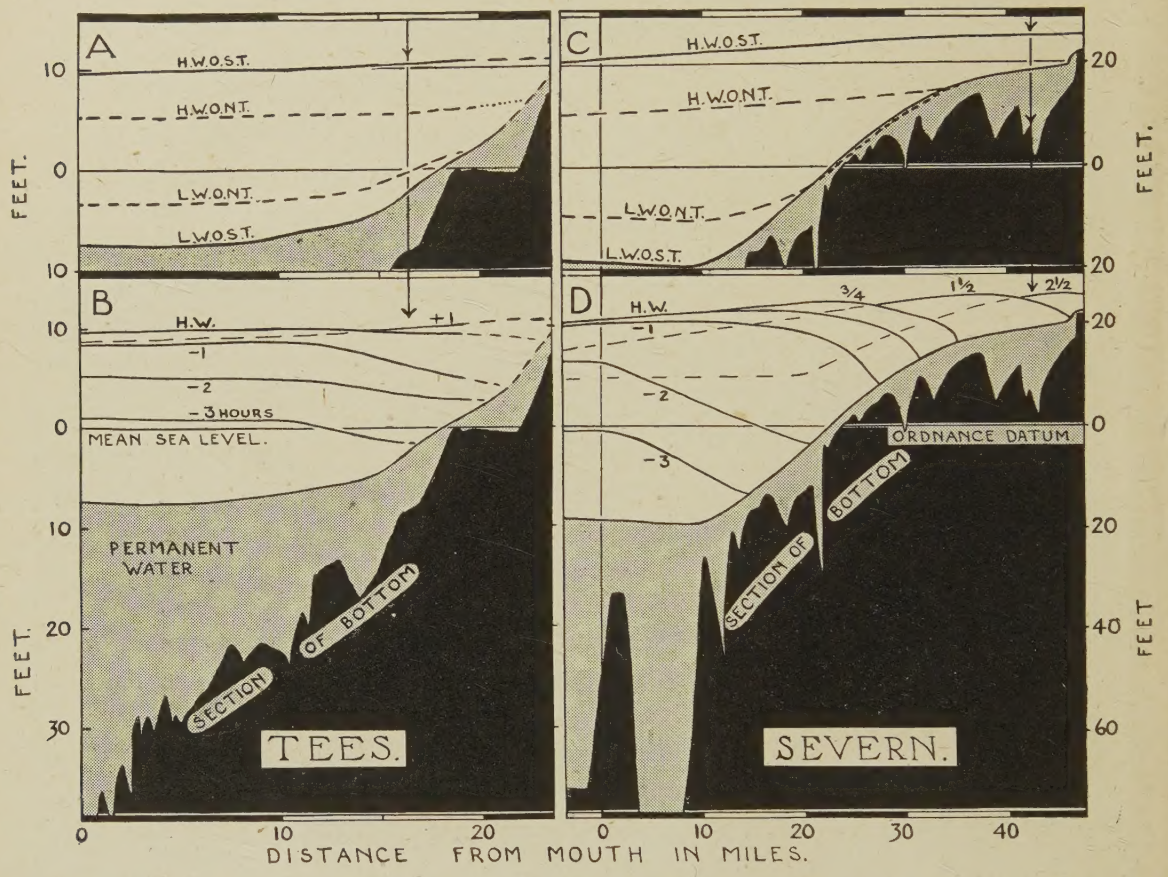

Fig. 1. A comparison of the tides of the Severn and Tees estuaries. A and B. Longitudinal sections of the Tees showing (A) the levels of high and low water of spring and neap tides and (B) the successive levels of the rising tide at 3, 2, 1 and 0 hr. before, and at 1 hr. after high water at 1½ miles from the sea. The arrow indicates the maximum limit of salt water penetration. C and D. Similar diagrams for the Severn, the successive levels in D being at 3, 2, 1 and 0 hr. before, and at ¾, 1½ and 2½ hr. after high water at Avonmouth and Aust. Data from Admiralty sources (Denman, 1931; Gibson, 1933) and from the Tees Conservancy Commission.

(*b*) *General salinity variations*

In the salinity curves given in Bassindale (1942, Fig. 1B), the vertical distance between the high- and low-water curves gives the change of salinity during the tide considered. By plotting these values we obtain curves showing the magnitude of the changes under varying conditions (Fig. 2A). The zone of maximum variation of salinity moves between Aust and Epney (10 and 35 miles) according to season and tidal range.

It has long been known that if the salt content of the water in which they are living is changed sufficiently slowly, many animals can acclimatize themselves to large changes. Thus, although the magnitude of the change is important the rate of change is also significant. In Fig. 2A the changes of salinity of up to 15·5 g. per litre (g.p.l.) take place during a single tidal period. But this period varies in different regions, and although the flood and ebb tide together take approximately 12·4 hr. in all parts of the estuary, with only minor variations, the flood tide occupies less and less of this period as the estuary is ascended until at Upton the 'ebb' flows all the time. This reduction in the duration of the flood tide is shown in Fig. 2B and differs for spring and neap tides.

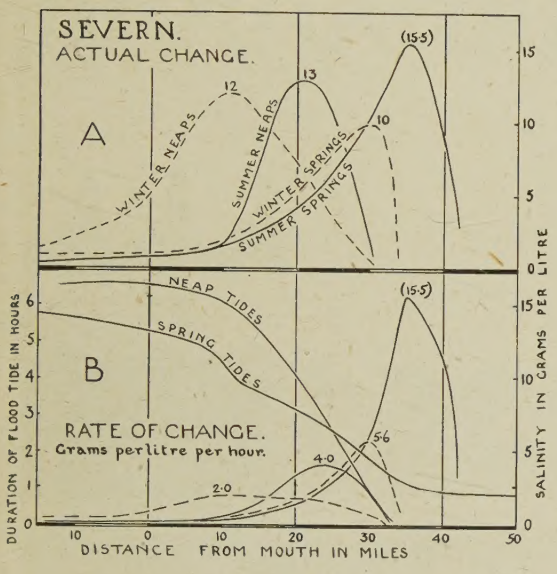

Fig. 2. Graphs showing the actual changes and the rates of change of salinity along the Severn estuary at different times (original data). The lower graphs include curves showing the duration of the flood tide during neaps and springs (Admiralty data, Gibson, 1933).

From the changes of salinity per tide and the minimum duration of flood or ebb it is possible to calculate the maximum rate of change of salinity under varying conditions and these rates are shown in Fig. 2B. Although the actual changes of salinity show similar maxima under varying conditions (from 10 to 15 g.p.l.) the rates of change show wide variations from 2 g.p.l. per hour (g.p.l.p.h.) at Aust during winter neap tides to 15·5 g.p.l.p.h. at Epney (35 miles) during summer spring tides. At Aust, however, the change endures for 6 hr. giving a total change of 12 g.p.l., whereas at Epney the change lasts only 1 hr. (on the flood) and gives a total change of only 15·5 g.p.l.

(Because the full account of the Severn estuary is not yet published it is necessary at this point to direct attention to the fact that salinity observations above Arlingham (30 miles) are scanty. The extension of curves showing salinity changes above Arlingham are based on the mainly hypothetical extensions of the salinity curves shown in Fig. 1B (Bassindale, 1942). Thus the maximum figure of 15·5 g.p.l. and 15·5 g.p.l.p.h. is a reasonable deduction from available data and not a direct determination.)

(*c*) *Salinity variations at specified stations*

In order to appreciate the effect on an animal living at a given place, it is necessary to arrange the data presented above in a different form. For this purpose conditions at Weston, Aust and Arlingham are illustrated in Fig. 3 and apply to any animal living at or below L.W.M. at these stations. (An animal living between tide marks is subject only to the higher salinities recorded.)

At Weston the salinity never changes more than 1 g.p.l. during a tide and in summer the change is less than 0·1 g.p.l. There is a gradual seasonal change however from about 22 to 28 g.p.l. The details of probable changes taking place during June are shown at A, B and C (Fig. 3).

At Aust the conditions are more complicated. During the summer the general level of salinity is about 25 g.p.l. and despite the strong tide flowing and ebbing through the Aust narrows the change of salinity is only 1 or 2 g.p.l. per tide. During spring tides in winter there is a similar small salinity change although the general level is much lower at 14 g.p.l. During neap tides the high-water salinity is of the order of 12 g.p.l., but the low-water salinity is much affected by the heavy fresh-water flow and may on rare occasions fall to zero. In Fig. 3 B and C for Aust the effect of the shortened duration of the spring-tide flood is apparent in the form of the curves.

At Arlingham Passage the salinity conditions are probably the most arduous in the river. In winter the water is always fresh at low tide and rises at high water up to 2 g.p.l. on neap tides and 10 g.p.l. on spring tides. In the dry season the water is fresh only at low water of neap tides and the salinity may be as high as 12 g.p.l. during low water of spring tides. The corresponding high-water salinities are 2 and 22 g.p.l. Thus, although the maximum change observed during a single tide was of the order of 15 g.p.l. (taking place at the rate of 15 g.p.l.p.h.) the changes occurring in one week would range from zero at low water of neap tides to 22 or even 25 g.p.l. at high water of spring tides. The corresponding change in winter is from zero to 12 or 14 g.p.l.

It is apparent that the salinity conditions at Weston are stable whilst those at Arlingham are very unstable and are most variable during the summer. At Aust the conditions are intermediate. During the present survey fifty-two species of intertidal animals have

been recorded from Weston, thirty-four from Aust and five from Arlingham. At Aust there is an extreme abundance of the hydroids *Sertularia cupressina* (L.) (of the *argentea* type) and of dwarf *Tubularia indivisa* L. These animals die down in winter and flourish only in summer. An examination of the salinity curves shows that by this means they avoid the unstable winter conditions with low salinities and

3. A COMPARISON OF THE SEVERN AND TEES

(*a*) *Size*

The Tees is smaller than the Severn and differs in its sudden debouchment into the North Sea. The Severn opens out gradually by way of the Bristol Channel, and the position of the mouth is more or

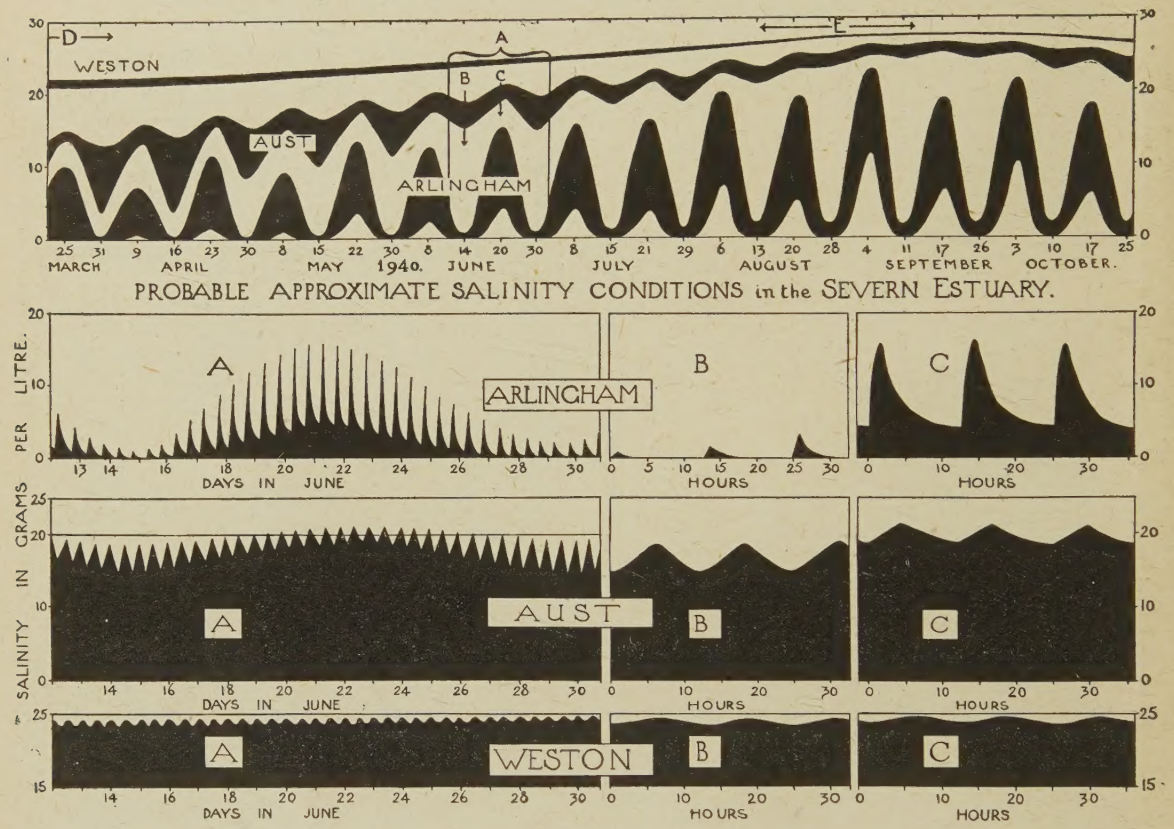

Fig. 3. A chart to illustrate the salinity conditions throughout the year 1940 at Weston, Aust and Arlingham Passage on the Severn estuary. Above are shown the variations from March to October, one black strip for each place. The upper limit of each black strip represents the high-tide salinity and the lower limit the low-tide salinity at the specified station. Actual observations are available only for one month each in winter and summer (periods D and E) and the intermediate conditions have been modified according to the range of tide predicted in Arrowsmith's Bristol Channel tide tables for 1940. Below, the actual changes of salinity are shown for the period A (12 June to 1 July) and at B and C are shown the changes during neap and spring tides respectively for the period marked on the upper diagram. The form of the curves C for Arlingham are sketched from the known range of salinity and the form of the tide curve given by Gibson (1933).

grow only when conditions are fairly stable and salinities reasonably high.

In a general way it is believed that excessive rainfall during the summer would cause the 'winter' type of salinity conditions to develop, but it is probable that these conditions would only persist for a few days and, although they would adversely affect the fauna, the normally hardy estuarine species would doubtless survive.

less arbitrarily fixed at King Road, Avonmouth. (This choice has been made by the Admiralty in their Charts as a boundary of areas of jurisdiction. The salinity and biological data show that below this point there is a reasonably stable salinity regime and a fairly numerous marine fauna; above this point the salinity varies widely, the fauna is sparse and intertidal banks hem in the channel. It seems, therefore, that King Road is the point corresponding most

closely to the 'mouth' of an estuary such as the Tees, which debouches direct into the sea and not into a long channel like the Bristol Channel.) The distance from the mouth to the limit of tidal action is 25 miles in the Tees and 66 miles in the Severn. This difference may be accounted for partly by the increased range of tide in the Severn, where a maximum of close on 50 ft. compares with a value of 18 ft. in the Tees. The slope of the estuary bed may also influence the length of the estuary and differences are apparent, since in the Severn neap tides penetrate only half-way along the estuary (to Framilode at about 35 miles), whereas in the Tees neap tides penetrate at least 20 miles or four-fifths of the spring tide penetration. It will be pointed out later that maximum salt water penetration is more nearly equal at about two-thirds of the full distance, this being above the effect of neap tides in the Severn but below it in the Tees.

From the point of view of salinity conditions the actual size of the estuaries is probably not so important as the relation of fresh-water flow to size of estuary. This relation is difficult to determine and available data are limited. The importance of the comparison make it necessary to attempt an estimate, and in order to emphasize the approximate nature of the values obtained the method of calculation will be given.

Rainfall figures for the Severn watershed and continuous gaugings of the Severn at Bewdley (involving the flow from about half the watershed) are available, and Gibson (1933) has calculated a mean flow for the Severn at Gloucester of 4270 cu. ft. per sec. (cusecs). The Wye discharges into the estuary above its mouth and its flow is given as 2000 cusecs.

From regularly spaced cross-sections the Severn Barrage Committee (1933) have estimated that the flow of tide past Severn Beach (5 miles above the mouth) is 24,500, 19,500 and 12,800 million cu. ft. on spring, ordinary and neap tides respectively. In estimating the capacity of the estuary to half-tide level one can find from Fig. 1 that the permanent water below low water of ordinary tides would have a volume of between one-quarter and one-half of the mean tide flow. From L.W.M. to half-tide level would be less than half the tidal flow, and so the capacity of the estuary to half-tide level above Severn Beach is estimated as between three-quarters of, and equal to the mean tide flow or between 14,600 and $19{,}500 \times 10^6$ cu. ft.

Thus the relation of estuary capacity (within the limits named) to the fresh-water discharge in 24 hr. is between $14{,}600 \times 10^6$ and $19{,}500 \times 10^6 : 6270 \times 3600 \times 24$ or between 27:1 and 36:1.

The capacity of the Tees estuary to mean sea level between 11 and 2·7 miles from the mouth and excluding certain tidal banks is given as 446×10^6 cu. ft. (Alexander and others, 1935). This determination is based on regular cross-sections. Assuming that the 2·7 miles near the mouth corresponds to the part of the Severn below Severn Beach which was not included in the above calculations, and adding 10% for the estuary above Stockton, a value of 490×10^6 cu. ft. is obtained for the Tees estuary capacity.

The flow of the river Tees has been closely studied (Butcher, Longwell & Pentelow, 1937) and values of 10–20 million cu. ft. per 24 hr. in summer and 40 to 50 million cu. ft. in winter are given. Assuming a mean flow of 30 million cu. ft., a mean fresh-water discharge of 347 cusecs compares with the Severn and Wye value of 6270 cusecs.

It can now be calculated that the Severn and Wye fresh-water discharge is 18 times that of the Tees and that the estuary is 30 to 40 times larger. The capacity of the Severn estuary is 27 times the fresh-water discharge in 24 hr. and the corresponding value for the Tees is 16 times. It should follow therefore that the fresh-water flow of the Tees has a greater effect on the estuarine salinity distribution than occurs in the Severn. This deduction is probably not invalidated by the approximate nature of these calculations, since the disproportion of the two estuaries is so great.

(*b*) *The tides*

Diagrams comparing the tides of the Severn and Tees are given in Fig. 1. It will be noticed that the proportions of vertical to horizontal scales are the same, but that the scales for the Tees are double those for the Severn.

In the Tees the crest of the tide wave does not rise, nor does the level of low water fall so markedly as in the Severn. The rising tide does not develop so steep a surface gradient, and correlated with this the maximum currents in the Tees are about 3 knots, whereas in the Severn 6 or even 8 knot currents may be recorded.

(*c*) *Salinity distribution*

Since curves for winter spring and neap tide salinities are not available for the Tees, Fig. 4 shows the distribution of salinity in the Tees and the Severn for summer and winter mean conditions and for spring and neap tides in summer only. The conditions in the Tees are for L.W.M. only.

There is much less difference in the Tees during summer between springs and neaps than in the Severn. This is probably due to the different relations in the two estuaries between the penetrations of salt water and of neap tides (see above, Fig. 1) as well as to the greater stability of conditions occasioned by the vertical salinity gradient of the Tees (see below).

In the Tees and Severn a spring tide carries salt water higher up the estuary than does a neap tide; but in the Tees the spring ebb carries the salt water farther seaward than does the neap ebb. That this is not the case in the Severn has been attributed by Beechey (1851) to the fact that the large volume of

salt water which is carried into the narrow reaches of the estuary during spring tides has insufficient time to drain away during the ebb. Thus not only are spring-tide low-water levels above Sharpness higher than neap-tide low-water levels, but the low-water salinities all along the estuary are correspondingly higher during springs and indeed exceed the neap-tide high-water salinities.

Despite the calculations given above and the deduction that fresh-water flow in the Tees should affect the salinities more than in the Severn the reverse is actually the case. This is undoubtedly partly due to the summer penetration by salt water of the narrow reaches of the Severn which in winter

Fig. 4. Graphs comparing the salinity conditions in the Tees and Severn estuaries. Tees diagrams redrawn from data in Alexander *et al.* (1935). Severn data original. The upper limit of each shaded zone represents the high tide salinity and the lower limit, the low tide salinity. The Tees mean salinities are from numerous observations when the upper river was below 1 ft. on the Croft gauge (summer condition) or between 1 ft. and 2 ft. 6 in. (winter condition). The Severn means are from daily samples at high and low water during March and August 1940. The curves *A* and *B* are repeated at *A′* and *B′* for comparison.

are only capable of conveying the flood water seawards. Thus salt has no chance of penetrating these reaches in winter. In addition, however, the development of a vertical salinity gradient in the Tees is known to provide an easy seaward passage for flood waters, leaving bottom waters relatively unaffected. This tends to produce a stability of salinity conditions which is not possible in the Severn.

(*d*) *General salinity variations and the vertical salinity gradient of the Tees estuary*

In the Tees the maximum salinity change per tide is much greater (Fig. 5) than in the Severn (Fig. 2), amounting to 23 g.p.l. The rate of change, however (Fig. 5), is only between 4 and 5 g.p.l.p.h. This low rate of change is due to the fact that salt water does not penetrate into those reaches of the Tees in which the duration of the flood tide has become reduced to 1 or 2 hr.

In the Severn estuary the salinity of bottom and surface waters is always the same at a given time and place. In the Tees, however, the bottom waters are

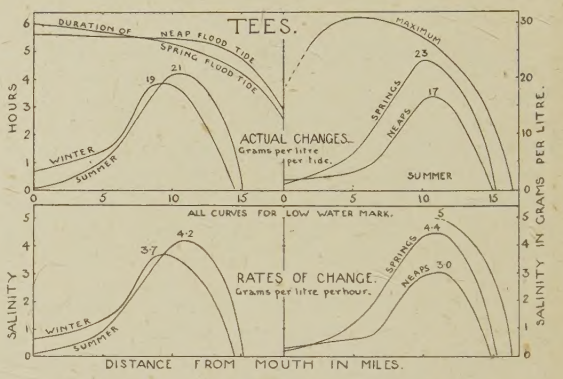

Fig. 5. Graphs derived from curves in Fig. 4, showing changes and rates of change of salinity at low water mark in the Tees estuary. The 'maximum' curve shown gives the maximum range ever recorded, but this does not apply to a single tide, except probably between 10 and 15 miles from the sea. It sets the outside possible maximum for any curve. All curves recalculated from data in Alexander and others (1935). The curves showing the duration of the flood tide are from diagrams in Denman (1931).

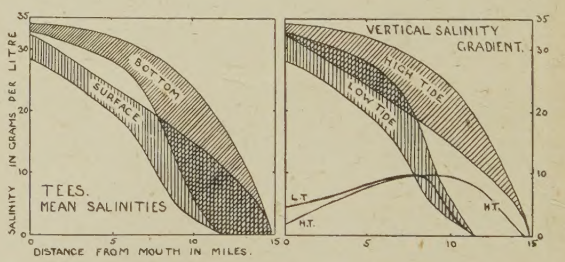

Fig. 6. Graphs showing the mean salinities at high and low tide of the bottom and surface waters in the Tees estuary. Identical curves shaded to show (left) the tidal variation on the bottom and at the surface and (right) the extent of the vertical salinity gradient at low tide (L.T.) and high tide (H.T.). Redrawn from Fig. 2 in Alexander and others (1935).

usually more saline than the surface waters. This is the vertical salinity gradient (V.S.G.) and animals living at different levels at the same station are subject to different salinity conditions irrespective of the differences occurring at different levels between tide marks.

The extent of the difference in salinity between bottom and surface waters is illustrated by the mean annual curves shown in Fig. 6. These are shaded in two ways to show (*a*) the extent of the difference of

salinity on the bottom and at the surface between high and low tide, and (*b*) the extent of the difference of salinity at high and low tide between surface and bottom waters. The bottom salinities are consistently higher than the surface values and the V.S.G. is at its maximum about 8 or 10 miles from the mouth.

The changes and rates of change of salinity for L.W.M. and bottom waters are given in Fig. 7. (These are derived partly from Fig. 4 and partly from data not republished here, and are not derived from Fig. 6, since the surface values are at different levels according to the state of tide.) The following points are clear:

(1) The maximum changes of salinity occur about 10 miles from the mouth and are about 20 g.p.l. per tide.

(2) The position of maximum variation on the bottom is slightly up-river of the L.W.M. maximum. This is correlated with the generally higher bottom salinities.

(3) Winter floods affect L.W.M. more than the bottom.

(4) The normal maximal rates of change of salinity lie between 4 and 5 g.p.l.p.h. on the bottom as well as at L.W.M.

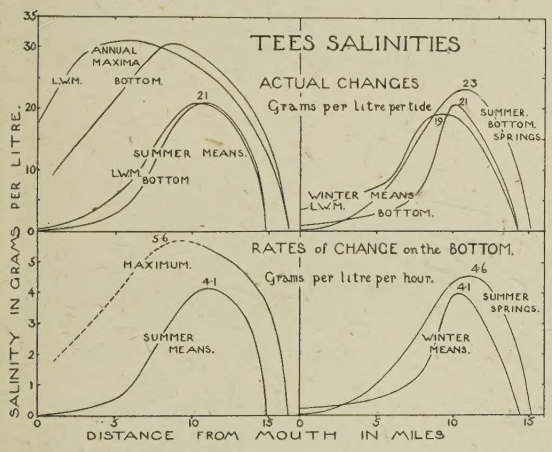

Fig. 7. Curves showing the changes and rates of changes of salinity at L.W.M. and on the bottom of the Tees estuary. Curves for L.W.M. derived from Fig. 4; for the bottom from similar unpublished curves. All data from Alexander and others (1935).

Milne (1938) has shown for the Tamar, which has a vertical salinity gradient, that at a given place the changes of salinity during a tide are greatest at L.W.M. and decrease up to H.W.M. and down to the bottom. This picture is, however, incomplete and, although the conditions described are found in the seaward part of the estuary where marine animals are normally found, they do not obtain above a certain point. In Fig. 7 the salinity variation curves cross near the point of maximum variation some 10 miles from the sea and above this point to the limit of salt-water penetration (16 miles) the greatest change of salinity takes place on the bottom. Milne's conditions are found from the sea to the point of maximum variation.

(*e*) *Salinity changes at specified stations*

For the Tees separate diagrams are necessary to show salinity conditions at L.W.M. and on the bottom. These are given in Fig. 8 for stations at 2, 10, 14 and 16 miles from the mouth and may be compared with the Severn diagrams in Fig. 3.

The conditions at 2 miles are like those at Weston. They show similar high salinities and are stable. There is, however, some variation with range of tide, the bottom salinities being less variable than the surface values. The larger variations occur during spring tides in winter.

At 12 and 14 miles from the sea the water is always fresh at low tide, but may be up to 23 and 13 g.p.l. respectively at high tide. There is considerable response to range of tide in the high water salinities. The greatest changes of salinity in the estuary occur 10 miles from the sea. The low-water salinities are below 10 and the high-water salinities above 20 g.p.l. Thus, although not subjected to fresh water (except during heavy floods and then only at L.W.M., not on the bottom) nor to pure sea water, animals at this station must suffer changes on *every tide* greater than 15 and rising to 23 g.p.l. or even more. This is a greater range than occurs during a single tide on the Severn, but it must be recalled that on the Severn the maximum rate of change is higher (15 instead of 5 g.p.l.p.h.) and in addition the range during one week in summer is from 0 to 25 g.p.l. On the other hand, the higher salinities, e.g. those above 15 g.p.l., must be endured for 2 or 3 hr. on the Tees but less than an hour on the Severn.

4. DISCUSSION

The severity of salinity conditions in the Tees and Severn has been estimated and it is not easy to say which of the two is the more arduous ecologically. It is perhaps of value to note that in the Tees those animals which are subjected to the largest changes are not subjected to zero salinities. In both estuaries animals are rare in the central reaches.

Experiments on the effect of changes of salinity on certain marine or brackish water animals have been done by several workers, and Wells and Ledingham (1940) point out that the worms *Arenicola marina* and *Nereis diversicolor* seem able to withstand changes greater than those found in the field and that changes taking place at a rate greater than 15 g.p.l.p.h. have no serious effect on these animals. Nevertheless, they admit that their experiments did not show why *Arenicola* could live in Baltic water of a salinity lower than the dissected tissues could withstand. They postulated the presence of a Baltic brackish water variety. This may be the case,

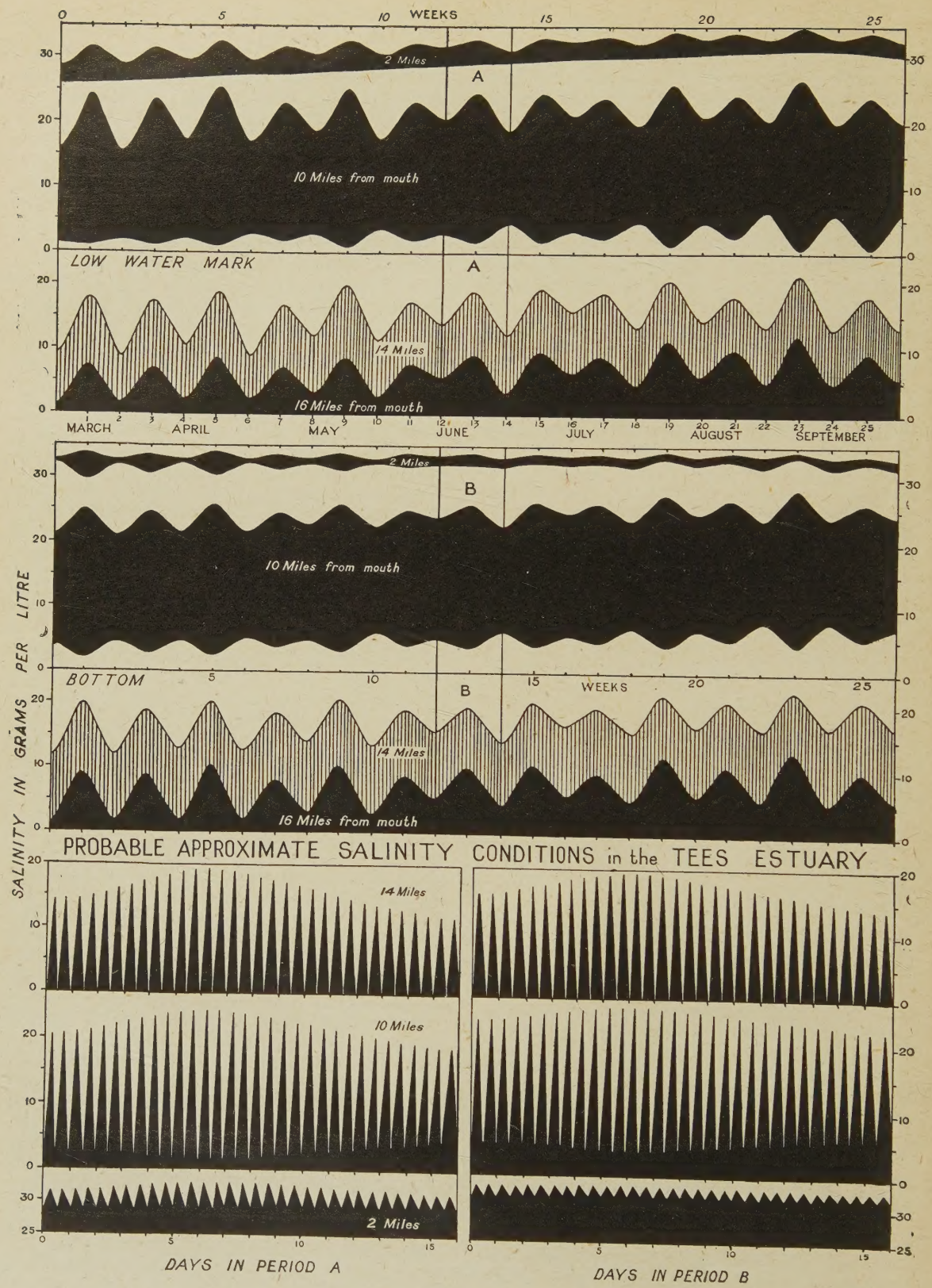
WEEKS
2 Miles
A
10 Miles from mouth
LOW WATER MARK
14 Miles
16 Miles from mouth
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
B
BOTTOM
SALINITY IN GRAMS PER LITRE
PROBABLE APPROXIMATE SALINITY CONDITIONS in the TEES ESTUARY
DAYS IN PERIOD A
DAYS IN PERIOD B

Fig. 8.

but it may also be true that the Baltic animals have merely been subjected to that acclimatization to which many marine animals are susceptible, when the changes of salinity are sufficiently slow. In addition, daily repeated changes of salinity of a magnitude known to occur in estuaries might easily have a cumulative effect and so restrict an animal to higher salinities than would be indicated by experiments involving only one or a few changes of salinity.

Finally, there are other adverse factors in an estuary, of which no mention has yet been made. Of these, current strength and the associated turbidity of the water and instability of the estuary bed are important. It is not proposed to deal with these here, but it may be mentioned that they all have maximum adverse values in the middle reaches of an estuary, just where the salinity changes and rates of change are also at a maximum. It follows therefore that in experiments dealing with only one factor such as salinity, an animal may show greater tolerance than its estuarine distribution indicates. This may be due to the added disadvantages of strong currents, turbid waters or sedimentation as well as to the above postulated cumulative effect of the twice daily repeated changes of salinity.

Where animals live in more arduous conditions in the field than under experiment the observations of Reid (1929), Alexander and others (1935) and of Milne (1940) may be recalled. These workers have shown that, by burrowing or closing up, an animal may avoid for a limited period the ill effects of temporary dilution of the water and so not be subject to the extremes of the observed variations. Limited migrations might achieve the same result.

5. SUMMARY

A brief account of the tidal conditions in the Severn and Tees is followed by more detailed accounts of the salinity variations throughout the estuaries. The following points are made:

(1) The Severn tide wave and salinity distribution are described briefly (Fig. 1B of Bassindale, 1942).

(2) Actual changes of salinity in the Severn vary from less than 1 to a maximum of 10 g. per litre (g.p.l.) during winter spring tides or to a maximum of 15·5 g.p.l. during summer springs (Fig. 2A).

(3) The rate of change of salinity in the Severn varies from nearly zero to a maximum of 2·0 g.p.l. per hour at Aust during winter neaps and to an (estimated) maximum of 15·5 g.p.l.p.h. at Epney during summer springs (Fig. 2B).

(4) Details of salinity changes at Weston, Aust and Arlingham (Fig. 3) show that (*a*) Weston has stable salinity conditions with a variation never greater than 1 g.p.l. per tide and a seasonal variation of about 6 g.p.l.; Aust has stable summer conditions with a general salinity of 25 g.p.l. and a variation of about 2 g.p.l. per tide. In winter the variation on spring tides is of 2 g.p.l. per tide at about 14 g.p.l. actual salinity, but on neap tides the variation is up to 10 g.p.l. per tide and the salinity may occasionally fall to zero; Arlingham has exceptionally arduous salinity conditions and an animal living there may be subject in summer to maximum variations of 15 g.p.l. per tide, at a maximum rate of 15 g.p.l.p.h. and in addition a variation within a week from zero to 25 g.p.l. The conditions at Aust are most stable under the high salinities attained during summer, and at Arlingham they are most stable under the low salinities occasioned by the winter floods.

(5) The Tees is a much smaller river than the Severn: the fresh-water flow is 18 times less: the estuary is 30 or 40 times less and the fresh-water flow in 24 hr. of the Severn is 27 times less than the capacity of the estuary (within certain limits), whereas the comparable Tees figure is 16.

(6) The tide wave of the Tees is compared with that of the Severn (Fig. 1).

(7) The effect on salinity distribution of tidal range and of winter floods is greater in the Severn than in the Tees. This is unexpected, since the Tees has the larger relative fresh-water flow. The result is bound up with the relatively greater penetration of salt water in the Severn on spring tides.

(8) The maximum variation of salinity is 17–23 g.p.l. per tide in the Tees. This is greater than in the Severn (Fig. 5).

(9) The maximum rate of change of salinity is considerably less in the Tees than in the Severn (5 compared with 15 g.p.l.p.h.). This also is bound up with the greater penetration of salt water in the Severn.

(10) The Tees has a vertical salinity gradient (V.S.G.), i.e. the bottom waters are more saline than the surface waters. This feature probably contributes to the stability of salinity condition in the Tees (see (7) above).

(11) The salinity conditions at specified stations show the features mentioned in (8) and (9) above (Fig. 8).

(12) The maximum salinity variations at any one station occur at L.W.M. in the lower reaches of the estuary (Milne, 1938 and Fig. 7) but above a given position to the limit of salt penetration the greatest variations occur on the bottom.

Legend to Fig. 8

Fig. 8. A chart to illustrate salinity conditions in the Tees estuary at stations 2, 10, 14 and 16 miles from the mouth. The extreme conditions shown are mean summer and winter conditions given by Alexander and others (1935) and the chart is built up as in Fig. 3. Conditions on the bottom and at low water mark are given separately and the details shown in B and C of Fig. 3 are omitted because there is no significant disparity between the duration of flood and ebb tides for the stations shown. The curves *A*, *A* are for L.W.M. and *B*, *B* for bottom waters.

(13) Salinity variations in the estuaries of the Severn and Tees are not so great as those withstood by animals under experiment (Wells and Ledingham, 1940). Two precautions must be observed in comparing experimental and field observations: (*a*) in the field an animal may avoid extreme variations in the environment by burrowing or closing up or by limited migrations, and (*b*) the continued twice daily repetition in the field of experimentally determined sublethal changes may have a cumulative effect.

6. ACKNOWLEDGEMENTS

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THE EMERGENCE RHYTHM OF THE DUNG-FLY, *SCOPEUMA* (=*SCATOPHAGA*) *STERCORARIA* (L.)

By C. B. LEWIS and J. D. BLETCHLY

(With 1 Figure in the Text)

1. INTRODUCTION

The objects of this investigation were, to discover whether an emergence rhythm exists in *Scopeuma* (=*Scatophaga*) *stercoraria* (Diptera, Cordyluridae) and, if a rhythm exists, to ascertain the effect of environmental conditions upon it. It was hoped that the records might form an interesting comparison with work done on the emergence of the Mediterranean flour-moth, *Ephestia kühniella* Zeller (Lepidoptera, Phycitidae); *Drosophila melanogaster* Meig. (Diptera, Drosophilidae); gall-midges (Cecidomyiidae); and other insects.

We are indebted to Prof. G. D. Hale Carpenter, D.M., for laboratory facilities in the Hope Department of Entomology, University Museum, Oxford, where these experiments were carried out, and to Dr B. M. Hobby and Mr H. N. Southern for very kindly reading the proofs.

2. HISTORICAL

Many people have recorded times of emergence for certain insects, but few have kept any continuous records. It would seem that emergence takes place, if it can be accomplished quickly, at the most favourable time for adult activity; if emergence is a lengthy procedure, it will begin long enough before the usual activity time, to permit the insect to be ready for flight when conditions are favourable.

Barnes (1930), working on Cecidomyiidae, wrote: 'Different species of midge emerge at different hours of the day. The emergence of the individuals of a species extends over several hours, and attains its maximum in numbers at a time which is constant for any one species.' He found that males usually emerge slightly before the females both in time of day and time of year. Barnes concluded that light played an important part in determining the time of day at which emergence shall take place.

Bremer (1926) kept *Ephestia kühniella* in the dark during the day and then exposed them to artificial light during the night. Under this treatment 60% of the moths, which usually emerge in the evening, emerged in the morning. Temperature was not controlled in Bremer's experiments, but he concluded that the reduction of light was the factor initiating emergence. In constant darkness, however, emergence continued as under normal lighting fluctuation, showing that inherent factors probably existed.

Scott (1936) found that the diurnal emergence rhythm of *E. kühniella* showed a close relationship with the diurnal temperature rhythm; the maximum emergence occurred shortly after the temperature began to fall. The rhythm continued, however, when larvae and pupae were moved into the constant-temperature rooms; the third generation reared in constant conditions still showed the rhythm; from which he concluded that it was inherited. Scott found, however, that by altering the time of minimum temperature new emergence rhythms could be set up.

3. BREEDING TECHNIQUE

Scopeuma stercoraria is in many ways an animal very suitable for laboratory studies, and it might well be used more extensively in physiological and genetical experiments. It is obtainable in England at all times of the year and is easily reared in the laboratory. In these experiments breeding was carried out in large glass jars (capacity about 3 qt.). Pieces of broken stone were placed at the bottom of the jar to allow for aeration and drainage; these were covered with a layer of soil on which cow dung was placed. (For other types of dung as breeding media see Cotterell (1920).) The supply of dung for the nutriment of the larvae must be adequate, and this has a considerable bearing on the size of the adults produced. The open end of the jar was covered over by a piece of muslin secured by an elastic band. This allowed ventilation and easy removal of the flies as they emerged.

4. DESCRIPTION OF EMERGENCE

The puparium has been well described by Cotterell (1920). Contrary to him, we found that pupation occurred more often in the dung itself than in the soil beneath.

Emergence was accomplished with the assistance of the ptilinum which by contractions and expansions broke open the puparium and, by the same process, forced an exit through the dung. The time elapsing from the first appearance of the head of the fly at the surface of the dung until the insect was entirely free was usually about 15 min.; shortly afterwards the ptilinum was retracted into the head.

If the dung had become dry, however, emergence took much longer and the ptilinum often persisted for half an hour. If the fly was still unsuccessful in its efforts to release itself, the ptilinum continued to show its rhythmical pulsations for 6 hr. or more, after which the fly usually died with the ptilinum still extruded. In general, the percentage of males which failed to emerge successfully was higher than the percentage of females.

The structure and function of the ptilinum of *S. stercoraria* is similar to that of the blow-fly, *Calliphora erythrocephala* (Meig.) (Tachinidae), as described by Laing (1935). A detailed description of the musculature of the ptilinum is in preparation.

5. DESCRIPTION OF EXPERIMENTS

Scopeuma stercoraria was being bred in the laboratory for anatomical work, and the decision to study the emergence was an incidental side-line. Thus, in the first instance (Exps. 1A and 1B), experimental conditions were not set up until just at the time when the flies were beginning to emerge. Four breeding jars were placed in a fume cupboard which was divided into two halves. One side, which contained jars 1 and 2, was fitted with white paper on three of the walls, and the floor was screened from daylight and illuminated by a 60 W. bulb placed 2 ft. from the glass front (Exp. 1B); the other side into which jars 3 and 4 were put was kept under the normal daylight conditions existing in the laboratory (Exp. 1A). The conditions of humidity were presumed to remain approximately constant, as the jars were kept very moist.

The two chief criticisms which should be made regarding this experiment were: (*a*) the control jars were under rather dim daylight conditions, and (*b*) the temperature in the constant-illumination chambers tended to be several degrees higher, on account of radiation from the electric-light bulb. The temperature fluctuations on the two sides were similar, however. The conditions were set up at 12.00 hr. on 2 May 1939 and the first observation was made 3 hr. later. A summary of the facts obtained regarding emergence under constant illumination and daylight conditions are given in tabular form (Exps. 1A and 1B). Jar 4 was rather unsatisfactory as it became stagnant and rather putrid, in consequence producing less flies.

The data from this set of jars showed that a rhythm existed and encouraged us to perform a more carefully planned second experiment. Exp. 2 was commenced on 22 May. In this instance twelve breeding jars were fitted up in the fashion described above; dung with eggs was placed in the jars. Two days later the jars were distributed as follows: four (jars 1–4) in the constant illumination chamber in the fume cupboard, four (jars 9–12) in a separated room near the window as daylight controls, and four (jars 5–8) in a photographic dark room under constant darkness. The conditions of humidity were about the same, but the differences in temperature were rather more marked than before and more especially the fluctuations. The data are presented in a table (Exps. 2A, 2B and 2C). Jar 11 is not included in the records since it became stagnant and putrid. Unfortunately, all-night watches were not kept until the 11th, so that the first counts on the mornings of the 9th and 10th tended to give a deceptively high figure.

Since the flies were never given enough time after emerging to dry their wings and become active, they were easily removed from the jars by means of forceps. The pill boxes, assigned one to each jar, served as lethal chambers, for here the flies were chloroformed, then sexed and counted. Temperatures were taken on Fahrenheit thermometers, and are given in that form, as they thus show fluctuations better than if converted to the Centigrade scale. It was necessary, of course, to use the electric light at intervals to examine jars in the dark room when emergence began.

6. RESULTS AND DISCUSSION

The figures indicate that in *Scopeuma stercoraria* there is a marked emergence rhythm, mainly reaching its peak between 09.00 and 14.00 hr. each day; practically no flies emerged during the night, between 20.00 and 06.00 hr. There is also a difference in emergence time between the sexes. Unlike the Cecidomyiidae studied by Barnes (1930), the females of *S. stercoraria* appeared first; the male emergence, generally speaking, seemed to be about a day in phase behind the females, and finally only males were found emerging from a culture. There appeared to be no differences in the hour of day for emergence of the sexes. Considering mating habits it is difficult to see any reason for the sexual difference in emergence, since the males are not attracted towards the females at first, and, according to Cotterell (1920), not for the first three weeks of their life. A cannibalistic habit may provide the explanation for the difference in the time of emergence of the two sexes; if food is not supplied to the males, which are markedly larger than the females, they will attack the latter and devour them. The majority of females, by getting a day's start over the males, have hardened their sclerotized parts, caught their first prey and gained full activity, making them less likely victims than if the sexes emerged together. It is also probable that maturation of the oocytes takes longer in a female than the attainment of the corresponding male maturity.

The control of environmental conditions did not appear to affect one sex more than the other. In view of this fact it is possible to examine the effects of the controlled conditions on both sexes together. (We are here considering only the data obtained from Exp. 2.)

Exp. 1 A. *Emergence under normal daylight fluctuation*

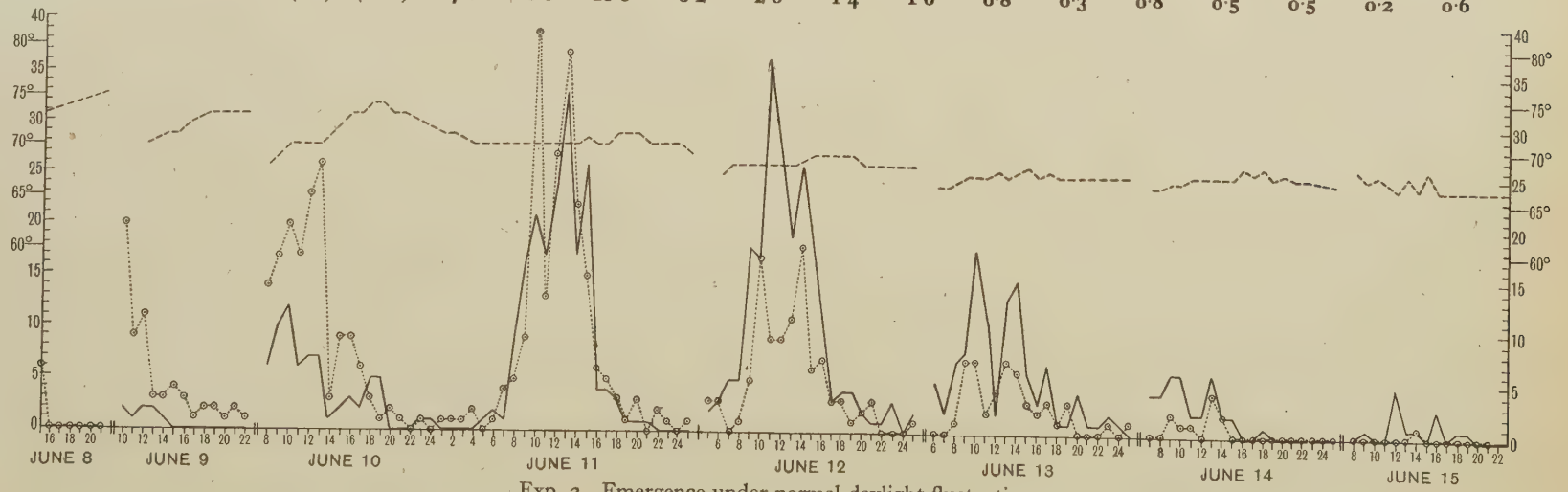
(Figures in italics are temperatures in degrees Fahrenheit; the others are numbers emerged during previous period)

Date May	Time (hr.) ...	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
2	♂	.	.	.	.	.	.	.	0	0	0	0	0	0	0	1	.
	♀	.	.	.	.	.	.	.	0	1	1	0	0	2	0	0	.
3	♂	0	0	1	3	0	0	1	0	0	1	0	0	0	0	.	.
	♀	0	2	5	3	1	3	1	0	0	1	0	0	2	0	.	.
4	♂	.	.	0	5	3	2	0	0	1	0	0	0	0	0	0	0
	♀	.	.	3	2	2	3	0	0	0	0	0	1	1	1	0	0
5	♂	.	.	1	4	6	2	2	0	1	1	0	0	0	0	0	.
	♀	.	.	2	2	2	4	3	1	1	1	1	0	0	0	0	.
	T.	.	.	*58*	*59*	*59*	*60*	*61*	*61*	*62*	*62*	*63*	*64*	*64*	*64*	*63*	.
6	♂	.	.	3	1	2	3	1	0	0	1	0	1	0	0	0	0
	♀	.	.	1	2	4	1	1	1	0	0	0	2	0	1	1	0
	T.	.	.	*59*	*61*	*62*	*63*	*64*	*64*	*64*	*63*	*63*	*63*	*63*	*63*	*63*	*63*
7	♂	.	.	1	1	1	2	1	0	1	1	0	0	0	0	1	.
	♀	.	.	1	2	4	3	2	1	0	0	0	1	0	0	0	.
	T.	.	.	*59·5*	*60*	*61*	*61*	*62*	*63*	*64*	*65*	*66*	*66*	*67*	*66*	*64*	.
8	♂	.	.	4	2	3	1	2	0	1	0	0	1	0	0	0	.
	♀	.	.	1	0	1	3	1	1	0	0	0	0	0	0	0	.
	T.	.	.	*57*	*59*	*59*	*60*	*61*	*62*	*64*	*65*	*65*	*65*	*65*	*65*	*65*	.
9	♂	.	2	1	6	4	0	2	1	0	0	2	0	0	0	.	.
	♀	.	0	4	1	0	0	1	0	0	0	0	0	0	0	.	.
	T.	.	*61·5*	*62*	*62*	*63*	*63*	*64*	*65*	*66*	*68*	*68*	*69*	*69*	*69*	.	.
10	♂	.	.	8	1	1	2	0	0	0	1	0	.	.	.	.	.
	♀	.	.	1	1	0	0	0	1	0	0	0	.	.	.	.	.
	T.	.	.	*67*	*67*	*67*	*68*	*68*	*69*	*70*	*70*	*70*	.	.	.	.	.
11	♂	.	0	1	2	0	0	0	0	0	1	.	.	.	.	.	.
	♀	.	0	0	0	0	0	0	0	0	1	.	.	.	.	.	.
	T.	.	*66*	*66*	*66*	*66*	*66*	*66*	*66*	*66*	*66*	.	.	.	.	.	.
Daily av. no.	♂	(0·0)	(1·0)	2·2	2·8	2·2	1·3	1·0	0·1	0·4	0·6	0·2	0·3	0·0	0·0	0·3	(0·0)
	♀	(0·0)	(1·0)	2·0	1·4	1·6	1·9	1·0	0·5	0·2	0·4	0·1	0·5	0·6	0·3	0·2	(0·0)
	♂+♀	(0·0)	(2·0)	4·2	4·2	3·8	3·2	2·0	0·6	0·6	1·0	0·3	0·8	0·6	0·3	0·5	(0·0)

Exp. 1 B. *Emergence under constant illumination*

(Figures in italics are temperatures in degrees Fahrenheit; the others are numbers emerged during previous period)

Date May	Time (hr.) ...	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
2	♂	.	.	.	.	.	.	.	0	0	0	0	0	0	0	0	0
	♀	.	.	.	.	.	.	.	0	0	1	0	0	0	0	0	0
3	♂	0	2	1	1	0	1	0	1	0	0	0	0	0	2	.	.
	♀	2	8	6	2	0	5	1	0	0	1	1	0	0	1	.	.
4	♂	.	.	5	2	2	0	0	0	1	0	0	2	0	0	0	0
	♀	.	.	6	10	10	7	0	1	3	0	0	0	1	0	0	2
5	♂	.	.	7	1	12	2	2	3	2	1	0	2	0	0	1	.
	♀	.	.	2	4	11	6	4	3	2	1	1	0	0	0	0	.
	T.	.	.	*60*	*61*	*62*	*62*	*62*	*62*	*63*	*64*	*65*	*65*	*65*	*65*	*65*	.
6	♂	.	.	4	14	7	8	2	1	1	1	0	0	2	0	0	0
	♀	.	.	1	2	1	0	0	0	0	0	0	0	0	0	0	0
	T.	.	.	*62*	*63*	*63·5*	*65*	*66*	*66*	*66*	*65*	*65*	*65*	*65*	*65*	*65*	*65*
7	♂	.	.	3	8	7	2	0	0	1	0	0	0	0	0	0	.
	♀	.	.	0.	0	0	0	1	0	0	0	0	0	0	0	0	.
	T.	.	.	*62·5*	*63·0*	*63·0*	*64·0*	*65·0*	*66·0*	*66·0*	*66·7*	*67·5*	*67·5*	*68·5*	*67·5*	*66·0*	.
Daily av. no.	♂	(0·0)	(2·0)	**4·0**	**5·2**	**5·6**	**2·6**	**0·8**	**0·8**	**0·8**	**0·3**	**0·0**	**0·6**	**0·3**	**0·3**	**0·2**	**0·0**
	♀	(2·0)	(8·0)	**3·0**	**3·6**	**4·4**	**3·6**	**1·2**	**0·6**	**0·8**	**0·5**	**0·3**	**0·2**	**0·2**	**0·2**	**0·0**	**0·6**
	♂+♀	(2·0)	(10·0)	**7·0**	**8·8**	**10·0**	**6·2**	**2·0**	**1·4**	**1·6**	**0·8**	**0·3**	**0·8**	**0·5**	**0·5**	**0·2**	**0·6**



Exp. 2. Emergence under normal daylight fluctuation.

⊙·····⊙ Total number of females ——— Total of males -------- Temperature (in degrees Fahrenheit)

Exp. 2A. *Emergence under normal daylight fluctuations*

(Figures in italics are temperatures in degrees Fahrenheit; the others are numbers emerged during previous period)

Date June	Time (hr.)...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
8	♂	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0	0	0	.	.	.
	♀	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	0	0	0	0	0	0	.	.	.
	T.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*73·0*	*73·3*	*73·6*	*74·0*	*74·3*	*74·6*	*75·0*	.	.	.
9	♂	.	.	.	.	.	.	.	.	.	2	1	2	2	1	0	0	0	0	0	0	0	0	.	.
	♀	.	.	.	.	.	.	.	.	.	20	9	11	3	3	4	3	1	2	2	1	2	1	.	.
	T.	.	.	.	.	.	.	.	.	.	*?*	*?*	*70·0*	*70·5*	*71·0*	*71·0*	*72·0*	*72·5*	*73·0*	*73·0*	*73·0*	*73·0*	*73·0*	.	.
10	♂	.	.	.	.	.	.	.	6	10	12	6	7	7	1	2	3	2	5	5	0	0	0	1	1
	♀	.	.	.	.	.	.	.	14	17	20	17	23	26	3	9	9	6	3	1	2	1	0	1	0
	T.	.	.	.	.	.	.	.	*68·0*	*69·0*	*70·0*	*70·0*	*70·0*	*70·0*	*71·5*	*72·5*	*73·5*	*73·5*	*74·5*	*74·5*	*73·5*	*73·5*	*73·0*	*72·5*	*72·0*
11	♂	0	0	0	0	1	2	1	5	9	21	17	24	33	17	26	4	4	3	1	1	1	0	0	0
	♀	1	1	1	2	0	1	4	9	16	39	13	27	37	22	15	6	5	3	1	3	0	2	1	0
	T.	*71·2*	*71·2*	*71·0*	*70·5*	*70·5*	*70·5*	*70·5*	*70·5*	*70·5*	*70·5*	*70·5*	*70·5*	*70·5*	*70·5*	*71·0*	*70·5*	*70·5*	*71·5*	*71·5*	*71·5*	*70·5*	*70·5*	*70·5*	*70·5*
12	♂	0	.	.	.	2	3	5	5	18	17	36	27	19	26	19	11	3	4	4	2	1	1	3	0
	♀	1	.	.	.	3	3	0	0	5	17	9	9	11	18	6	7	3	3	1	2	3	0	0	0
	T.	*69·5*	.	.	.	*67·5*	*68·5*	*68·5*	*68·5*	*68·5*	*68·5*	*68·5*	*68·5*	*69·0*	*69·5*	*69·5*	*69·5*	*69·5*	*69·5*	*69·0*	*68·5*	*68·5*	*68·5*	*68·5*	*68·5*
13	♂	2	.	.	.	.	5	2	7	8	18	11	2	13	15	6	3	7	1	1	4	1	1	2	1
	♀	1	.	.	.	.	0	0	1	7	7	2	4	7	6	3	2	3	1	3	0	0	0	1	0
	T.	*68·5*	.	.	.	.	*66·5*	*66·5*	*67·0*	*67·5*	*67·5*	*67·5*	*68·0*	*67·5*	*68·0*	*68·5*	*67·5*	*68·0*	*67·5*	*67·5*	*67·5*	*67·5*	*67·5*	*67·5*	*67·5*
14	♂	0	.	.	.	.	.	4	4	6	6	2	2	6	2	2	0	0	1	0	0	0	0	0	0
	♀	1	.	.	.	.	.	0	0	2	1	1	0	4	2	0	0	0	0	0	0	0	0	0	0
	T.	*67·5*	.	.	.	.	.	*66·7*	*66·7*	*67·0*	*67·0*	*67·5*	*67·5*	*67·5*	*67·5*	*67·5*	*68·5*	*68·0*	*68·5*	*67·5*	*68·0*	*67·5*	*67·3*	*67·2*	*67·1*
15	♂	0	.	.	.	.	.	.	0	1	0	0	5	1	1	0	3	0	1	1	0	0	0	0	.
	♀	0	.	.	.	.	.	.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	.
	T.	*67·0*	.	.	.	.	.	.	*68·5*	*67·5*	*68·0*	*67·0*	*66·5*	*68·0*	*66·5*	*68·5*	*66·5*	*66·5*	*66·5*	*66·5*	*66·5*	*66·5*	*66·5*	*66·5*	.
Daily av. no.	♂	0·4	(0·0)	(0·0)	(0·0)	(1·5)	3·3	3·0	4·5	8·7	10·9	10·4	9·9	11·6	9·0	6·9	3·0	2·0	1·9	1·5	0·9	0·4	0·3	1·0	0·4
	♀	0·8	(1·0)	(1·0)	(2·0)	(1·5)	1·3	1·0	4·0	7·8	14·9	7·3	10·6	12·6	7·9	5·4	3·4	2·2	1·5	1·0	1·0	0·7	0·4	0·5	0·0
	♂+♀	1·2	(1·0)	(1·0)	(2·0)	(3·0)	4·6	4·0	8·5	16·5	25·8	17·7	20·5	24·2	16·9	12·3	6·4	4·2	3·4	2·5	1·9	1·1	0·7	1·5	0·4

Exp. 2B. *Emergence under constant illumination*

(Figures in italics are temperatures in degrees Fahrenheit; the others are numbers emerged during previous period)

Date June	Time (hr.)...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
9	♂	.	.	.	.	.	.	.	.	.	0	0	1	0	0	0	0	0	0	0	0	0	0	.	.
	♀	.	.	.	.	.	.	.	.	.	3	1	0	1	2	0	1	0	0	0	0	0	0	.	.
	T.	.	.	.	.	.	.	.	.	.	*70·0*	*69·5*	*69·0*	*69·5*	*70·5*	*71·0*	*72·0*	*72·5*	*72·5*	*72·5*	*73·0*	*72·5*	*72·5*	.	.
10	♂	.	.	.	.	.	.	.	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0
	♀	.	.	.	.	.	.	.	0	0	0	5	0	1	0	0	0	0	0	0	0	0	0	1	0
	T.	.	.	.	.	.	.	.	*63·5*	*64·5*	*64·5*	*64·5*	*65·0*	*65·5*	*67·0*	*68·0*	*69·5*	*70·0*	*71·0*	*71·5*	*71·5*	*70·5*	*70·5*	*69·5*	*69·5*
11	♂	0	0	0	0	0	0	0	0	0	2	0	1	1	6	1	1	0	0	0	0	0	0	0	0
	♀	0	0	0	0	0	0	0	0	0	5	2	1	9	15	4	7	1	1	0	1	0	0	0	0
	T.	*69·0*	*67·5*	*67·0*	*66·5*	*67·0*	*67·0*	*67·0*	*66·5*	*66·5*	*66·0*	*65·5*	*65·0*	*65·0*	*65·5*	*65·5*	*65·5*	*65·5*	*66·0*	*66·5*	*66·5*	*66·5*	*66·0*	*65·5*	*65·5*
12	♂	0	.	.	.	0	0	0	0	2	1	0	3	8	4	2	3	1	2	2	4	1	0	0	0
	♀	0	.	.	.	0	0	0	0	1	0	3	7	7	10	7	17	7	8	4	9	2	0	1	0
	T.	*64·5*	.	.	.	*61·5*	*61·5*	*61·5*	*61·5*	*61·5*	*62·5*	*63·0*	*63·0*	*63·5*	*64·0*	*64·0*	*65·0*	*66·0*	*66·0*	*65·0*	*66·0*	*66·0*	*65·0*	*65·0*	*64·5*
13	♂	0	.	.	.	.	0	0	0	0	1	0	8	5	8	9	4	9	3	4	2	2	1	0	1
	♀	0	.	.	.	.	1	0	0	1	0	2	4	6	14	10	9	20	5	5	2	1	1	0	1
	T.	*63·5*	.	.	.	.	*58·0*	*59·0*	*59·0*	*59·0*	*59·5*	*60·0*	*60·0*	*60·5*	*61·0*	*61·0*	*61·0*	*62·0*	*62·0*	*62·2*	*62·0*	*62·5*	*62·5*	*62·5*	*62·5*
14	♂	0	.	.	.	.	.	1	0	2	0	5	9	14	13	8	9	6	6	0	1	2	0	0	0
	♀	0	.	.	.	.	.	0	0	1	1	5	12	23	18	1	8	9	2	5	6	0	0	0	0
	T.	*62·5*	.	.	.	.	.	*61·0*	*61·0*	*61·0*	*61·0*	*61·4*	*61·8*	*62·0*	*62·5*	*62·5*	*63·5*	*64·5*	*63·5*	*65·0*	*64·5*	*64·0*	*64·0*	*63·5*	*62·5*
15	♂	0	.	.	.	.	.	.	0	2	6	2	12	22	18	6	4	4	3	2	1	1	0	1	.
	♀	0	.	.	.	.	.	.	1	0	3	1	5	19	15	9	14	5	3	1	3	1	0	1	.
	T.	*62·5*	.	.	.	.	.	.	*61·5*	*61·0*	*61·0*	*61·0*	*61·5*	*62·0*	*62·0*	*62·0*	*62·0*	*62·0*	*62·0*	*62·5*	*62·5*	*62·0*	*62·0*	*62·0*	.
16	♂	.	.	.	.	.	.	.	4	2	4	10	17	7	9	7	7	6	6	1	0	0	0	0	.
	♀	.	.	.	.	.	.	.	1	1	3	6	4	7	2	5	3	0	0	3	0	1	0	0	.
	T.	.	.	.	.	.	.	.	*?*	*?*	*61·0*	*61·0*	*62·0*	*62·0*	*62·0*	*62·0*	*62·0*	*62·0*	*62·0*	*62·8*	*62·5*	*62·0*	*62·0*	*61·0*	.
17	♂	.	.	.	.	.	.	.	3	1	2	6	10	6	9	3	0	4	0	0	3	2	1	1	.
	♀	.	.	.	.	.	.	.	1	1	1	3	5	3	4	1	0	2	0	0	1	0	1	1	.
	T.	.	.	.	.	.	.	.	*59·0*	*59·3*	*59·5*	*60·0*	*60·5*	*61·0*	*62·0*	*62·5*	*62·5*	*62·7*	*63·0*	*63·0*	*63·2*	*63·2*	*63·8*	*64·0*	.
18	♂	.	.	.	.	.	.	.	.	4	5	5	2	1	1	1	1	0	0	0	0	0	0	.	.
	♀	.	.	.	.	.	.	.	.	5	0	1	0	3	2	1	0	0	0	0	0	0	0	.	.
	T.	.	.	.	.	.	.	.	.	*62·0*	*62·0*	*62·3*	*63·0*	*64·0*	*64·5*	*64·0*	*64·2*	*64·5*	*64·8*	*64·5*	*64·0*	*64·0*	*64·0*	.	.
19	♂	.	.	.	.	.	.	.	.	.	5	0	2	0	0	2	0	0	3	.	.	.	.	.	.
	♀	.	.	.	.	.	.	.	.	.	2	0	0	0	0	0	0	0	1	.	.	.	.	.	.
	T.	.	.	.	.	.	.	.	.	.	*59·0*	*59·5*	*60·0*	*61·0*	*61·5*	*62·5*	*63·0*	*63·5*	*64·2*	.	.	.	.	.	.
Daily av. no.	♂	**0·0**	**(0·0)**	**(0·0)**	**(0·0)**	**(0·0)**	**(0·0)**	**0·3**	**8·7**	**1·4**	**2·4**	**2·5**	**6·0**	**6·0**	**6·2**	**3·5**	**2·6**	**2·7**	**2·1**	**0·9**	**1·1**	**0·8**	**0·2**	**0·2**	**0·2**
	♀	**0·0**	**(0·0)**	**(0·0)**	**(0·0)**	**(0·0)**	**(0·3)**	**0·0**	**3·7**	**1·1**	**1·6**	**2·6**	**3·5**	**7·5**	**7·3**	**3·5**	**5·4**	**4·0**	**1·8**	**1·6**	**2·2**	**0·5**	**0·2**	**0·5**	**0·2**
	♂+♀	**0·0**	**(0·0)**	**(0·0)**	**(0·0)**	**(0·0)**	**(0·3)**	**0·3**	**12·4**	**2·5**	**4·0**	**5·1**	**9·5**	**13·5**	**13·5**	**7·0**	**8·0**	**6·7**	**3·9**	**2·5**	**3·3**	**1·3**	**0·4**	**0·7**	**0·4**

Exp. 2 C. *Emergence under total darkness*

(Figures in italics are temperatures in degrees Fahrenheit; the others are numbers emerged during previous period)

Date June	Time (hr.)...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
8	♂	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0	0	0	.	.	.
	♀	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	0	0	0	0	0	1	.	.	.
	T.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	*78·0*	*78·3*	*78·6*	*78·9*	*79·3*	*79·7*	*80·0*	.	.	.
9	♂	.	.	.	.	.	.	.	.	.	1	0	1	1	0	0	1	1	3	1	4	0	2	.	.
	♀	.	.	.	.	.	.	.	.	.	20	3	2	3	4	3	5	9	10	3	5	5	2	.	.
	T.	.	.	.	.	.	.	.	.	.	*73·0*	*73·6*	*74·2*	*74·6*	*75·0*	*74·7*	*75·0*	*76·0*	*76·0*	*76·0*	*76·5*	*76·5*	*76·0*	.	.
10	♂	.	.	.	.	.	.	.	14	0	12	7	7	8	8	4	6	9	1	2	0	2	1	0	0
	♀	.	.	.	.	.	.	.	25	0	9	4	5	8	7	4	2	3	1	0	3	0	0	0	0
	T.	.	.	.	.	.	.	.	*71·0*	*72·0*	*71·0*	*72·0*	*72·5*	*73·0*	*74·0*	*74·7*	*75·4*	*76·0*	*76·0*	*76·0*	*76·0*	*76·0*	*76·0*	*76·0*	*76·0*
11	♂	2	1	1	1	0	0	0	2	5	7	11	4	1	4	1	0	0	2	0	1	0	1	2	0
	♀	0	1	0	1	2	2	1	3	1	6	2	7	8	11	1	2	3	2	2	1	1	0	4	0
	T.	*75·5*	*75·0*	*74·5*	*74·0*	*73·8*	*73·3*	*73·0*	*72·5*	*72·5*	*73·0*	*73·0*	*73·0*	*73·0*	*73·5*	*73·0*	*74·0*	*73·5*	*73·5*	*74·0*	*74·0*	*74·0*	*73·0*	*72·5*	*72·0*
12	♂	0	.	.	.	2	0	0	2	3	5	4	2	9	7	1	7	1	1	1	1	1	0	3	1
	♀	2	.	.	.	2	0	2	1	3	6	4	20	5	10	1	6	4	3	4	5	1	2	1	4
	T.	*70·0*	.	.	.	*69·6*	*69·3*	*69·0*	*68·5*	*69·0*	*69·0*	*69·0*	*69·0*	*70·0*	*70·0*	*70·0*	*70·0*	*70·0*	*70·0*	*70·0*	*70·0*	*70·0*	*70·0*	*69·5*	*69·0*
13	♂	0	.	.	.	.	4	2	1	2	5	8	2	6	10	9	1	7	1	2	2	1	0	1	0
	♀	0	.	.	.	.	0	1	0	2	10	7	3	8	11	3	3	8	2	1	1	4	2	0	1
	T.	*68·5*	.	.	.	.	*68·5*	*68·0*	*68·0*	*66·5*	*68·5*	*66·5*	*67·0*	*67·0*	*67·0*	*67·0*	*67·0*	*67·5*	*67·5*	*67·5*	*67·5*	*67·5*	*68·0*	*68·0*	*67·5*	*67·0*
14	♂	1	.	.	.	.	.	1	2	3	5	7	7	12	7	3	3	1	2	2	3	0	0	1	3
	♀	1	.	.	.	.	.	1	1	2	4	6	5	12	12	0	3	2	7	0	2	0	1	0	0
	T.	*67·0*	.	.	.	.	.	*66·5*	*66·0*	*66·0*	*66·0*	*66·0*	*66·8*	*67·5*	*68·0*	*68·0*	*68·8*	*68·0*	*63·7*	*68·7*	*69·2*	*69·2*	*69·2*	*69·2*	*68·7*
15	♂	0	.	.	.	.	.	.	8	2	9	6	7	6	8	2	2	0	1	0	1	0	0	1	.
	♀	0	.	.	.	.	.	.	2	2	2	2	3	1	3	1	2	1	2	0	0	0	0	2	.
	T.	*68·5*	.	.	.	.	.	.	*67·0*	*67·5*	*67·5*	*67·0*	*67·0*	*67·0*	*67·0*	*68·0*	*67·0*	*67·5*	*67·0*	*68·0*	*68·0*	*67·0*	*67·0*	*67·0*	.
16	♂	.	.	.	.	.	.	.	1	2	2	2	3	4	1	1	2	3	0	1	0	1	0	0	.
	♀	.	.	.	.	.	.	.	3	2	3	2	1	1	0	1	2	4	2	2	0	0	0	0	.
	T.	.	.	.	.	.	.	.	*66·8*	*66·5*	*66·2*	*66·2*	*66·2*	*65·0*	*66·2*	*66·2*	*66·2*	*66·2*	*66·2*	*66·8*	*66·5*	*66·3*	*66·5*	*66·8*	.
17	♂	.	.	.	.	.	.	.	0	0	2	0	2	2	1	1	1	2	0	1	1	0	0	0	.
	♀	.	.	.	.	.	.	.	1	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	.
	T.	.	.	.	.	.	.	.	*64·8*	*64·5*	*64·0*	*64·5*	*65·0*	*66·0*	*66·7*	*66·7*	*66·2*	*66·5*	*66·8*	*66·8*	*66·8*	*67·0*	?	?	.
18	♂	.	.	.	.	.	.	.	.	0	1	0	0	0	0	0	0	0	1	0	0	0	.	.	.
	♀	.	.	.	.	.	.	.	.	0	0	0	1	0	0	0	1	0	0	0	0	0	.	.	.
	T.	.	.	.	.	.	.	.	.	*65·0*	*65·0*	*66·2*	*66·3*	*66·4*	*66·5*	*66·6*	*66·8*	*66·9*	*66·9*	*66·9*	*66·9*	*66·9*	.	.	.
Daily av. no.	♂	**0·6**	**(1·0)**	**(1·0)**	**(1·0)**	**(1·0)**	**(1·3)**	**0·7**	**3·8**	**1·9**	**4·9**	**4·5**	**3·5**	**4·9**	**4·6**	**2·0**	**2·1**	**2·2**	**1·1**	**0·9**	**1·2**	**0·5**	**0·4**	**1·0**	**0·8**
	♀	**0·6**	**(1·0)**	**(0·0)**	**(1·0)**	**(2·0)**	**(0·6)**	**1·2**	**4·5**	**1·3**	**6·1**	**3·1**	**4·8**	**4·8**	**5·8**	**1·5**	**2·4**	**3·1**	**2·6**	**1·1**	**1·5**	**1·1**	**0·8**	**0·9**	**1·0**
	♂ + ♀	**1·2**	**(2·0)**	**(1·0)**	**(2·0)**	**(3·0)**	**(1·9)**	**1·9**	**8·3**	**3·2**	**11·0**	**7·6**	**8·3**	**9·7**	**10·4**	**3·5**	**4·5**	**5·3**	**3·7**	**2·0**	**2·7**	**2·6**	**1·2**	**1·9**	**1·8**

There was a tendency for the jars under constant illumination and under constant darkness to have less pronounced peaks of emergence than the control daylight jars; their emergence rhythm tended to be more spread over the hours of the day, and the period of emergence continued over a larger number of days than that of the daylight jars. These two tendencies are most marked in the jars under constant darkness. Jars 7 and 8, particularly the latter, produced all their flies in a relatively short time, and the emergence throughout the day was more uniformly distributed than in jars 5 and 6.

Two secondary peaks of emergence were noticed, which occurred in an ascending order of lateness as follows: daylight, constant illumination and constant darkness. These were observed between 15.00 and 16.00 hr. and between 20.00 and 22.00 hr. in daylight; between 15.00 and 17.00 hr. and between 20.00 and 22.00 hr. under constant illumination; between 16.00 and 18.00 hr. and 20.00 and 24.00 hr. under constant darkness. Further data may show these peaks to be coincident and insignificant.

The evidence at hand suggests, therefore, that the normal daylight rhythm is at least a contributory factor in controlling the emergence rhythm of *S. stercoraria*, but further experiments are needed to show the extent of its importance.

Temperature appears to be an unimportant factor, but the evidence at hand cannot be taken as at all conclusive. It may be pointed out that in Exp. 1 (jars 3 and 4) there was a tendency for the time of the maximum emergence peak, in the case of the females, to be delayed on those days when the initial temperature was low. In Exp. 1 B the evidence is inadequate to permit any conclusions to be drawn on this point. In Exp. 2, under all conditions, the male and female peaks of emergence seem to be quite independent of temperature. The importance of temperature may be seasonal. During the colder part of the year temperature may be the factor initiating emergence, but during the warmer season, when the daily fluctuations remain more or less within the optimum limits, temperature may be unimportant. In Exp. 1 the temperature difference between the constant illumination and control daylight jars was more or less constant and showed similar fluctuations.

Since Exp. 2 started with the unhatched eggs, we knew the flies were of the same age. Unfortunately, experimental conditions were not set up immediately, but the jars were placed under them from an early larval stage (2 days). Temperature differences were more marked than in Exp. 1, usually amounting to about 3–5° F.; the fluctuations were sometimes quite different under the three conditions. It is to be noted, that in the dark room jars, where the most marked deviation from the normal emergence curve occurred, the temperature showed the least fluctuation throughout the 24 hr., although the general shape of the temperature curve resembles that of the daylight controls, with a similar range of fluctuation. In the constant-illumination jars the fluctuation was greatest.

7. SUMMARY

1. In the laboratory *Scopeuma stercoraria* shows a diurnal rhythm of emergence reaching its peak between 09.00 and 14.00 hr. each day; practically no flies emerged during the night between 20.00 and 06.00 hr.

2. Females of *S. stercoraria* appeared first; the male emergence, generally speaking, seemed to be in a phase of about a day behind the females and, finally, only males were found emerging from a culture.

3. The sexes showed no difference in the hour of day at which they emerged.

4. Control of environmental conditions did not appear to affect one sex more than the other.

5. Jars under constant conditions (light or darkness) showed less pronounced peaks of emergence than the control daylight jars.

6. The evidence suggests that the normal daylight rhythm is at least contributory in controlling the emergence rhythm of *S. stercoraria*.

7. Temperature appeared to be unimportant, but it is suggested that the extent of its importance may be seasonal.

8. The data suggest that a rhythm of emergence is inherited but that alteration of rhythmical environmental conditions can modify it.

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OBSERVATIONS AT A PIPISTRELLE BAT ROOST

By L. S. V. VENABLES, *Bureau of Animal Population, Oxford University*

(With 2 Figures in the Text)

1. INTRODUCTION

The Seacourt Stream leaves the river Thames at Northfield Farm, Wytham, and rejoins it again on the outskirts of Oxford, thus forming an 'island' roughly three miles long and half a mile wide. This island is very thinly inhabited. A mile from the south end is the small village of Binsey and half a mile farther north, completely isolated, Binsey Church and Church Farm. A few scattered barns, Medley Manor Farm towards the south and the ruins of Godstow Nunnery and two lock-keepers' cottages towards the north, complete the other buildings on the island. A number of ditches run across, and trees and hedges are plentiful, so that it is an ideal locality for numerous insects and therefore for the food supply of bats.

Elton & Middleton (in Hobby, 1939) give the following records for this island or its immediate vicinity:

Pipistrelle (*Pipistrellus pipistrellus*)
Noctule (*Nyctalus noctula*)
Whiskered bat (*Myotis mystacinus*)
Natterer's bat (*M. nattereri*)
Daubenton's bat (*M. daubentonii*)

I have identified at Binsey the pipistrelle (sight and five collected), noctule (sight), whiskered (sight), Natterer's (sight), Daubenton's (sight), long-eared bat (*Plecotus auritus*) (sight and three collected). On an evening in late September 1942, excellent views were had of a barbastelle (*Barbastella barbastellus*) hunting around the willow trees at the south of Port Meadow—on the opposite side of the Thames to Medley Manor.

The pipistrelle is common, and the main roost is in the church roof (346 emerging being my highest count). The five collected were from the church. About twenty noctules were to be seen on the wing during the summer evenings of 1940 and 1941, but only about half a dozen during the summer of 1942. Whiskered and Natterer's I have identified only twice each—being confident of the former species but not so much so with the latter. Daubenton's is thinly distributed along the willow-shaded Seacourt Stream and is occasionally to be seen hunting over the Thames. The long-eared bat can be seen anywhere in Binsey, but is very casual in its appearance and apparently far from common. It roosts occasionally in the church (see Table 1) but more frequently in the barns of Church Farm.

The pipistrelle roost at which these observations were made is situated in the narrow space (into which it is impossible to see) between the ceiling and the stone 'slates' of Binsey Church. This church is between a thick, swampy wood of oaks, elms and pollard willows and the buildings of Church Farm. It is surrounded by ditch-bordered grass fields and, as stated above, is isolated by half a mile from the rest of the village. A few bats emerge from the eaves and other odd cracks, but the vast majority come out of one chosen exit hole. In the summer of 1940 this was where a slate was missing on the top of the south-west corner of the roof; but in the spring of 1941 starlings built in this hole and the main bat exit then changed to the south bell-rope hole. This was also the exit in 1942. (It should be pointed out that the bells were not being rung during these years, owing to war regulations.) This one-hole emergence made a fairly accurate count easy, but on many occasions another observer would go round to the other side of the church to make sure that bats were not being missed there. Very few bats, however, were seen to emerge from the north side. I am particularly grateful to Mr E. J. Parkyns of Church Farm for frequent help in this and also for doing some independent counts of the main exit to check with mine, and for undertaking counts on a few occasions when I was unable to get there.

Roughly, I paid one visit per week excepting in the cold of the winter (two consecutive visits and three consecutive visits are bracketed in Table 1), arriving about half an hour before the first bat came out and staying until dark, which was well after the last bat had emerged. Full counts were taken during the 1940 and 1941 visits, but in the 1942 visits, which completed the two years' observations, only the time of the first bat was recorded, except for full counts on 4 June and 30 July. There was usually a lag of some minutes between the first bat or bats and the commencement of a steady exit, but the squeaking had reached a crescendo by the first emergence, so the bats were well awake to that time, light and temperature. The cessation of squeaking was a good guide as to when the last bat had left, but I always stayed on a good deal later than this, until it was too dark to see. There is little or no squeaking when the few late-in-the-season bats are waking and coming out.

All the data I obtained are given in Table 1. The various items are discussed individually below. Sun time at Long. 1°, Lat. 52° is used, this, and the times of sunset, being obtained from the *Nautical Almanac*.

Table 1

Date	At time of first emergence (if any): Temp. at 4 ft. ° F.	Condition of sky	Light (Weston reading above church)	Wind	Rain	Sun time at long. 1°, lat. 52°: Time of first bat	Time of last bat	Time taken to emerge in min.	Minutes before (B) or after (A) sunset of first emergence	No. of pipistrelle bats	No. of long-eared bats
19 July 1940	?	Clear	?	?	—	?	?	?	?	241	1
20 July 1940	?	Clear	?	?	—	?	?	?	?	247	1
3 August 1940	?	Clear	?	—	—	?	?	?	?	181	1
6 August 1940	60	Slight overcast	1·5	—	—	19.55	20.29	34	A 9	214	—
14 August 1940	57	Some clouds	1·0	—	—	19.34	20.08	34	A 3	128	1
21 August 1940	52	Clouds to west	0·75	Strong gusts	—	19.27	19.52	25	A 11	24	—
26 August 1940	57	Slight overcast	0·75	—	—	19.19	19.27	8	A 14	17	—
28 August 1940	56	Slight overcast	2·0	—	—	19.00	19.34	34	B 1	27	—
7 September 1940	57	Clear	1·5	Slight breeze	—	18.52	19.06	14	A 14	7	1
14 September 1940	57	Some clouds	0·75	—	—	18.35	18.49	14	A 13	7	—
19 September 1940	52	Heavy clouds	0·25	—	—	18.30	18.44	14	A 20	6	—
28 September 1940	43	Clear	0·25	Slight breeze	—	18.14	18.37	23	A 24	9	—
5 October 1940	52	Heavy overcast	0·25	Moderate breeze	—	17.48	17.56	8	A 15	7	—
11 October 1940	40	Clear	0·25	—	—	17.45	17.59	14	A 25	6	—
18 October 1940	46	Haze	0·25	—	—	17.36	17.41	5	A 32	8	—
24 October 1940	38	Clear	0·0	Very light	—	17.31	17.31	—	A 39	1 (Returned to roost in 7 min.)	—
1 November 1940	49	Slight overcast	0·0	Very light	—	16.51	16.54	3	A 15	2	—
9 November 1940	42	Heavy overcast	0·25	Slight breeze	Slight drizzle	16.30	?	?	A 8	1–2	—
15 November 1940	40	Overcast	—	Light breeze	—	—	—	—	—	—	—
23 November 1940	40	Clear	—	—	—	—	—	—	—	—	—
29 November 1940	29	Clear	—	—	—	—	—	—	—	—	—
8 February 1941	47	Slight overcast	2·0	Very light	—	16.52	16.52	—	B 12	1	—
15 February 1941	34	Slight overcast	—	—	Drizzle	—	—	—	—	—	—
21 February 1941	29	Clear	—	—	—	—	—	—	—	—	—
28 February 1941	40	Overcast	—	Very light	Drizzle	—	—	—	—	—	—
3 March 1941	40	Slight overcast	—	—	—	—	—	—	—	—	—
6 March 1941	40	Overcast	—	—	—	—	—	—	—	—	—
13 March 1941	38	Clear	0·0	Light breeze	—	18.41	18.41	—	A 37	1	—
15 March 1941	38	Clear	—	—	—	—	—	—	—	—	—
21 March 1941	46	Slight overcast	0·25	—	—	18.46	19.03	18	A 28	5	—
27 March 1941	40	Some clouds	—	—	—	—	—	—	—	—	—

4 April 1941	40	Slight overcast	?	—	—	19.14	19.19	5	A 32	2	—
10 April 1941	40·5	Slight overcast	?	—	—	19.09	19.43	34	A 17	4	—
12 April 1941	51	Slight overcast	?	Light breeze	—	19.16	19.31	15	A 21	6	—
17 April 1941	43	Clear	?	—	—	19.04	19.44	40	0	11	—
22 April 1941	46	Overcast	?	—	—	19.22	19.46	24	A 10	9–10	—
25 April 1941	39	Clear	—	Strong breeze	—	—	—	—	—	—	—
29 April 1941	42	Slight overcast	?	Light breeze	[illegible]	19.52	20.04	12	A 28	3	—
3 May 1941	37	Clear	?	[illegible]	[illegible]	20.04	20.19	15	A 33	3–4	—
9 May 1941	36	Clear	?	—	—	20.04	20.29	25	A 23	6	—
13 May 1941	48	Overcast	?	—	—	20.04	20.39	35	A 17	35	—
21 May 1941	45	Overcast	?	?	Drizzle	20.04	?	?	A 5	48	—
3 June 1941	49	Heavy overcast	2·0	—	—	20.14	21.04	50	B 2	233	1
10 June 1941	47	Heavy overcast	?	Strong gusts	Few spots	20.29	21.14	45	A 7	29	—
17 June 1941	60	Clear	0·75	—	—	20.46	21.34	48	A 20	206	1
23 June 1941	58	Slight overcast	?	—	—	20.48	?	?	A 20	46	—
30 June 1941	60	Clear	0·75	—	—	20.49	?	?	A 21	12	—
7 July 1941	62	Clear	0·5	[illegible]	[illegible]	20.50	21.09	19	A 26	8–9	—
13 July 1941	56	Clear	?	—	—	20.50	21.19	29	A 30	10	—
21 July 1941	59	Haze	?	—	—	20.14	20.43	29	A 3	18	—
3 August 1941	60	Clear	?	—	—	20.04	20.36	32	A 12	148	—
11 August 1941	57	Some clouds	4·0	Gusts	Few spots	19.28	20.14	46	B 9	83	—
15 August 1941	57	Overcast	1·0	—	—	19.32	20.14	42	A 3	103	—
16 August 1941	52·5	Clouds to west	1·0	—	[illegible]	19.35	20.16	41	A 8	98	—
17 August 1941	57·5	Heavy overcast	1·0	Light gusts	Few spots	19.19	20.01	41	B 6	74	—
22 August 1941	57	Clouds to west	12·0	—	—	19.09	19.56	47	B 6	93	—
31 August 1941	60	Clear	4·0	—	—	18.59	19.40	41	A 4	84	1
6 September 1941	57	Heavy overcast	0·5	Moderate gusts	Slight drizzle	18.49	19.24	35	A 8	60	—
13 September 1941	59·5	Overcast	1·0	Very light	—	18.29	18.55	26	A 4	51	—
18 September 1941	52	Clear	7·0	—	[illegible]	18.16	18.49	33	A 3	33	—
27 September 1941	65	Clear	1·25	—	—	18.09	18.29	20	A 17	18	—
2 October 1941	57·5	Haze	8·0	—	—	17.44	18.14	30	A 3	4	—
10 October 1941	54	Few clouds	1·5	Very light breeze	[illegible]	17.34	17.52	18	A 12	3	—
18 October 1941	55	Few clouds	0·5	Moderate	-	17.24	17.37	13	A 19	3	—
25 October 1941	45·5	Overcast	—	—	—	—	—	—	—	—	—
1 November 1941	39	Slight overcast		Moderate gusts	—	—	—	—	—	—	—
8 November 1941	44	Very slight overcast	5·0	—	[illegible]	16.24	16.47	23	0	3	—
14 November 1941	42	Fog	—	—	—	[illegible]	[illegible]	[illegible]	—	—	—
21 November 1941	49	Few clouds	—	—	—	—	—	—	-	—	—

Table 1 (*continued*)

Date	Temp. at 4 ft. ° F.	Condition of sky	Wind	Rain	Time of first bat	Minutes before (B) or after (A) sunset of first emergence	No. of pipistrelle bats	No. of long-eared bats
27 February 1942	35	Clear	—	—	—	—	—	—
3 March 1942	46	Overcast	Light to moderate breeze	Slight drizzle	—	—	—	—
9 March 1942	44	Slight overcast	—	—	—	—	—	—
15 March 1942	52	Slight overcast	—	—	18.34	A 27	?	?
23 March 1942	43	Clear	—	—	—	—	—	—
25 March 1942	52	Clear	—	—	18.39	A 15	?	?
30 March 1942	52	Clear	—	—	18.54	A 21	?	?
6 April 1942	49·5	Some clouds	Strong gusts	—	—	—	—	—
8 April 1942	45	Clear	—	—	19.24	A 36	?	?
13 April 1942	52	Few thin clouds	—	—	19.14	A 17	?	?
18 April 1942	54	Slight overcast	—	—	19.16	A 11	?	?
2 May 1942	46·5	Clear	—	—	19.49	A 20	?	?
9 May 1942	50	Clear	Light	—	20.05	A 25	?	?
16 May 1942	54	Clear	—	—	20.14	A 22	?	?
22 May 1942	56·5	Slight overcast	—	—	20.24	A 24	?	?
29 May 1942	50	Cloudy	—	—	20.11	A 1	?	?
4 June 1942	65	Clear	—	—	20.32	A 16	118	—
16 June 1942	52·5	Some clouds	—	—	20.41	A 15	?	?
24 June 1942	60	Slight overcast	Very light breeze	—	20.39	A 11	?	?
2 July 1942	68	Clear	—	—	20.39	A 12	?	?
8 July 1942	57	Some clouds	—	—	20.34	A 10	?	?
17 July 1942	58	Overcast	—	—	20.18	A 2	?	?
23 July 1942	62	Some clouds	Very light breeze	—	20.10	A 1	?	?
30 July 1942	59	Clear	—	—	19.59	0	346	2

2. RELATION OF ACTIVITY TO ENVIRONMENTAL FACTORS

(*a*) *Temperature.* Visits were paid to the roost only about once a week. Between visits the maximum-minimum temperatures might fluctuate wildly and one would have to go to the roost every night to find out the effect. One possible effect of day maximum was in mid-June to mid-July 1941, when there was an abnormal heat wave with readings up to 92° F. in the University Museum garden at Oxford. The heat must have been unbearable immediately below the stone slates at Binsey Church and the bat counts dropped from over 200 to about 10, partly recovering by the beginning of August. Possibly the colony moved to a roost with a cooler day temperature, but I was unable to locate this in any of the buildings, though they might have roosted in trees. Barrett-Hamilton (1910–11) records that both pipistrelle and long-eared bats sometimes change their roosting place in summer for a few weeks or even a few days.

If the counts (including records of 'none') are averaged in 5° temperature units, the relationship shows still more clearly:

Table 3

Temp. ° F.	No. of counts	Average no. of bats	Range of counts
25–29	2	0	—
30–34	1	0	—
35–39	8	1·4	0– 6
40–44	17	2·3	0– 11
45–49	13	28·4	0–233
50–54	7	25·3	3– 98
55–59	17	63·3	3–346
60–64	6	112·1	8·5–214
65–69	2	78·0	18–118

Barrett-Hamilton (1910–11) says: 'An evening temperature of 40° to 43° Fahrenheit is probably required to keep (the pipistrelle) at home.' Moffat (1904) says that in winter in Ireland, if the dusk

Table 2. *Dusk temperatures and individual bat counts*

(N.B. No counts from 22 November 1941 to 26 February 1942)

° F.		° F.		° F.	
29	0, 0	44	3, 0	55	3
30	—	45	48, 0, ✓	56	27, 10, ✓
31	—	46	8, 5, 9–10, 0, ✓	57	128, 17, 7, 7, 83, 103, 74, 93, 60, 4, ✓
32	—	47	1, 29	58	46, ✓
33	—	48	35	59	18, 51, 346
34	0	49	2, 233, 0, 0	60	214, 206, 12, 148, 84, ✓
35	0		(One of the 0 counts being probably due to strong, gusty wind)	62	8–9, ✓
36	6			63	—
37	3–4			64	—
38	1, 1, 0	50	✓, ✓	65	18, 118
39	0, 0	51	6	66	—
40	6, 0, 0, 0, 0, 0, 0, 2, 4	52	24, 6, 7, 98, 33, ✓, ✓, ✓, ✓, ✓	67	—
41	—	53	—	68	✓
42	1–2, 3, 0	54	3, ✓, ✓		
43	9, 11, 0				

✓ = Bats emerged, but no census done.

These 'summer swarms', as he calls them, '. . . cluster in outhouses where they are unknown throughout the rest of the year'. Allen (1939), during hot noonday sun, saw little brown bats (*Myotis lucifugus*), roosting in the peak of a New England barn, creep out and hang from the edges of boards inside the barn where it was cooler.

As to the counts in the present communication: minimum temperature would, no doubt, be very often shortly before dawn and maximum temperature around noon, but it is in the evenings that the bats awake and emerge, so it is dusk temperatures (at a height of 4 ft. in the churchyard) that are used here. The bats at this roost were mostly inactive at temperatures below about 40° F. It will be seen in Table 2 that when it was 40° or under at dusk, on 65 % of my visits no bats emerged and, when they did so, only in very small numbers. When it was 41° or over, on only 9·8 % of my visits did no bats come out. None came out at 35° or under, and at least some bats never failed to come out at 50° or over.

temperature is over 43°, some bats (apparently almost always pipistrelles) are fairly certain to be seen on the wing. Below 43° emergence is doubtful but sometimes takes place down to 39°. Barrett-Hamilton gives corresponding figures of 40° and 38° for an English roost.

(*b*) *Light.* I went 93 times to the roost and bats emerged on 73 of my visits. A light record was taken on 36 of the 73 occasions. A Weston exposure meter reading was taken of the sky immediately above the church as soon as the first bat emerged. This would be the amount of light shining in through the holes in the roof that were facing upwards (as the two main exit holes were).

Weston readings	No. of times they occurred
0·0 –0·50	13
0·51–1·0	10
1·1 –2·50	7
2·51–5·0	3
Over 5·0	3

Average of readings in February (mid-April no records), end of May to early June, August and after the first week of November (at which times the bats were emerging earlier than during the rest of the season):

16 readings: average 2·4

Average of readings for rest of season:

20 readings: average 1·27

(*c*) *Wind.* 'Popular' books on natural history sometimes state that bats do not like gusty winds. Observations at the roost, however, suggest that it is only some of the bats that avoid these conditions. There seems to be a reduction in numbers emerging, but not all the bats are prevented from coming out. Unfortunately, no counts were taken during rain except on a small number of occasions when a few rain spots or light drizzle was falling—too slight to prevent a hungry bat having its evening hunt. These data will be found in Table 1. Four of the examples coincide with gusty winds and a (presumably) corresponding falling off in bat numbers. These are marked with an asterisk in the section 'Wind'.

(*e*) *Time of emergence.* It will be seen from the general trend of the curves in Fig. 1 that the bats commence to emerge at about sunset by August but become progressively later towards either end of the season. It also suggests that earlier emergence takes place in February (one record only), mid-April, end of May or early June, and at the very end of the

	Temp. ° F.	Wind	No. of pipistrelles
14 August 1940	57	—	128
21 August 1940	52	Strong gusts	24*†
26 August 1940	57	—	17
22 April 1941	46	—	9–10
25 April 1941	39	Strong breeze	0‡
28 April 1941	42	Light breeze	3
3 June 1941	49	—	233
10 June 1941	47	Strong gusts	29
17 June 1941	60	—	206
3 August 1941	60	—	148
11 August 1941	57	Gusts	83*
15 August 1941	57	—	103
16 August 1941	52·5	—	98
17 August 1941	57·5	Light gusts	74*
22 August 1941	57	—	93
31 August 1941	60	—	84
6 September 1941	57	Moderate gusts	60*†
13 September 1941	59·5	Very light breeze	51
30 March 1942	52	—	Pipistrelle emerged. No census
6 April 1942	49·5	Strong gusts	0
8 April 1942	45	—	Pipistrelle emerged. No census

* See section 'Rain'. † Seasonal falling off in numbers taking place.
‡ In this case the dusk temp. was probably the chief factor.

Two exceptions to the latter point are in April, which is too early for a regular emergence of high numbers to have started.

The church is so well protected by trees that not much wind finds its way into the churchyard, on to which face the two main exits to the roost. It will be seen from Table 1 that such light breezes as got in appeared to make no difference to the numbers of bats emerging, but that there often seems to be a falling off when gusts of wind blew into the yard. Counts with gusty winds and the one count with a strong breeze are given above with the counts immediately before and after, but it should be remembered that the numbers of bats sometimes fluctuated at other times when there was no wind.

(*d*) *Rain.* Barrett-Hamilton says: 'All bats love shelter and are much impeded or entirely kept at home by foul weather even in summer, at which season it is probable that exceptional cold or wet causes the death of many from starvation.' Unfortunately, no counts were taken during rain except on a small number of occasions when a few rain spots or light drizzle was falling—too slight to prevent a hungry bat having its evening hunt. These data will be found in Table 1. Four of the examples coincide with gusty winds and a (presumably) corresponding falling off in bat numbers. These are marked with an asterisk in the section 'Wind'.

(*e*) *Time of emergence.* It will be seen from the general trend of the curves in Fig. 1 that the bats commence to emerge at about sunset by August but become progressively later towards either end of the season. It also suggests that earlier emergence takes place in February (one record only), mid-April, end of May or early June, and at the very end of the season in November. Heavy cloud cover is marked on the figure but it seems to be unimportant.

This (seemingly) regular earlier start to the night's feeding in August is an interesting point and, it seems, not so far studied for the pipistrelle. It is recorded of this species in notes by Coward & Oldham (1910) on their observations in Cheshire: 'The time of appearance relative to sunset varies according to season and weather; for instance, on January 8th we have noticed its first appearance at forty minutes after sunset, and at the end of April at thirty-six minutes after, whereas in May it has appeared on the wing at times varying from twenty minutes to thirty minutes after sunset; in June it has emerged a few minutes before or after sunset, and in July from ten minutes before to thirty minutes after. In the next three months we have seldom seen it abroad until after sunset, but on November 2nd we saw three on the wing at Knutsford a few minutes before sunset, and a week later a single bat flying

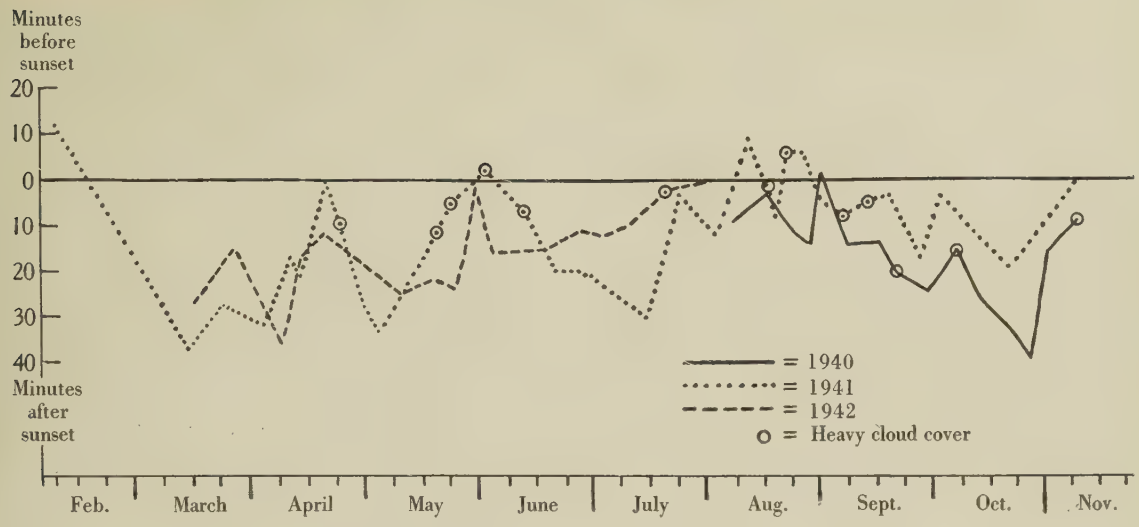

Fig. 1. Time of first bats' emergence in minutes before or after sunset.

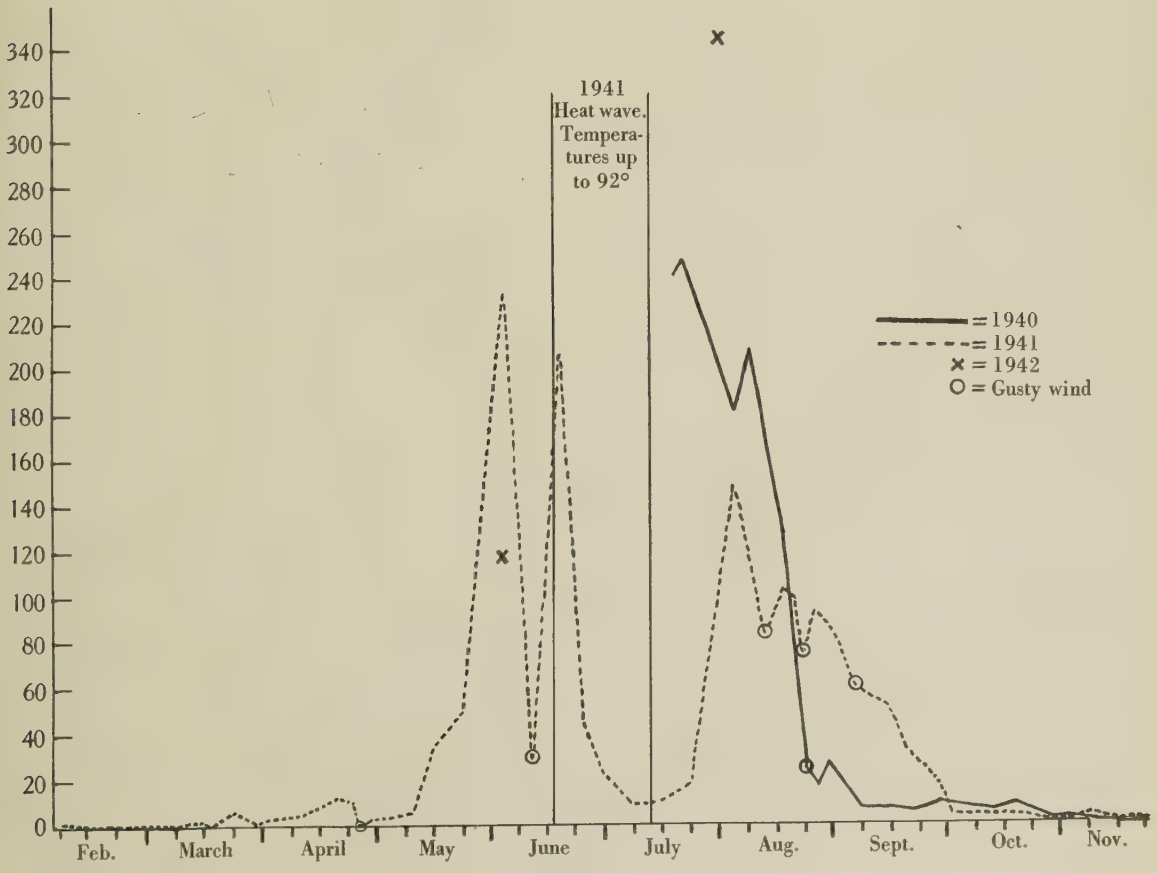

Fig. 2. Counts of total numbers of bats emerging from roost.

two hours before sunset.' Apparently the marked sunset emergence in August at this Oxfordshire roost does not apply to the roost (or roosts) studied by Coward in Cheshire.

Sandars (1937) says of the noctule: 'Time of evening flight varies with season.... In early spring it is 20 or 30 minutes before sunset, in mid-Aug. 7 minutes after, returning to the relatively earlier time in September.' On the other hand, Vesey-Fitzgerald (1941), writing also of the noctule, gives two examples—first exit 28 min. after sunset on 21 April to 7 min. before sunset on 14 August, and 37 min. after sunset on 2 April to 24 min. before sunset on 12 September. However, it is not much use quoting observations on other species to compare with those made on the pipistrelle, for Barrett-Hamilton states, for example, that the barbastelle precedes '...by some little time the pipistrelle, the long-eared bat and even the noctule'.

(*f*) *Amount of time taken for total number of bats to emerge from the roost.*

Total counts of	2– 9 bats.	20 records.	Av.	15·1	min.
,,	10– 24 ,,	7 ,,	,,	25	,,
,,	25– 49 ,,	4 ,,	,,	36·7	,,
,,	50– 99 ,,	7 ,,	,,	39·5	,,
,,	100–149 ,,	3 ,,	,,	36	,,
,,	150–250 ,,	4 ,,	,,	41	,,

(*g*) *Counts of pipistrelles emerging from roost throughout the season.* These are shown in Fig. 2. As is to be expected, only a few bats come out in the cold evenings of February to April and October to November, and the high numbers come out in May to August. There are, however, very big fluctuations in these high numbers. Some seem to be correlated with gusty winds (see section 'Wind') and one was possibly due to an abnormal heat wave in June-July 1941 (see section 'Temperature') which must have caused a well-nigh unbearable heat immediately below the stone slates. This heat wave and the counts with gusty winds are shown on Fig. 2.

3. SUMMARY

1. Visits were paid about once a week to a roost of pipistrelle bats (*Pipistrellus pipistrellus*) in a country church near Oxford. It was impossible to see into the roost, but counts were taken of the bats coming out at dusk. 346 was the highest count. All the data obtained are given in Table 1. Results are discussed under the following headings.

2. *Dusk temperature.* The threshold temperature for emergence appears to be usually above 40° F.

3. *Condition of sky.* Apparently unimportant.

4. *Light.* The first bat emerged with a Weston reading of 1·0 or under on 64 % of my observations. On only three occasions was the reading over 5·0.

5. *Wind.* Gusty winds seem to discourage some of the bats from coming out.

6. *Rain.* No data on heavy rain.

7. *Time of first emergence.* Around sunset in August, becoming progressively later towards either end of the season. The two seasons' data suggest that earlier emergence also takes place in February (one record only), mid-April, end of May or early June, and at the very end of the season in November.

8. *Time taken to emerge.* Total counts of 2–9 bats averaged 15 min. to emerge. 150–250 averaged 41 min.

9. *Counts of bats.* Small numbers came out in the cold evenings of February to April and October to November. The high numbers came out in May and August. Marked fluctuations in these high numbers seemed sometimes to be correlated with gusty winds and possibly once with a heat wave with temperatures up to 92° F.

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THE DISTRIBUTION OF THE FAUNA OF SOME INTERTIDAL SANDS AND MUDS ON THE NORTHUMBERLAND COAST

By F. BRADY

(With 10 Figures in the Text)

1. INTRODUCTION

The main object of the investigations was to determine the distribution of the fauna at various levels of the beach at different localities on the Northumberland coast. In addition, some of the more important factors of the environment of the animals collected were investigated, partly with the object of discovering what correlation, if any, existed between them and the distribution of the fauna, and partly to determine the existence of any unusual conditions. The consistency of the sand and the salinity and *p*H of the interstitial water were the main factors examined.

The laboratory work connected with the research was carried out at the Cullercoats Dove Marine Laboratory, and I am indebted to Prof. A. Meek, Mr B. Storrow, Dr H. O. Bull and Mrs Cowan for much encouragement and advice. I am also grateful to Prof. A. D. Hobson for valuable suggestions regarding the preparation of this paper.

2. COLLECTION OF FAUNA

At each locality chosen for investigation collections were usually made at intervals between L.W.M. and H.W.M. of an average spring tide.

A folding metal frame with sides 3 in. deep was pushed into the sand, enclosing an area of $\frac{1}{4}$ sq. m. The sand was then dug out in layers approximately 1 in. deep to determine the depths to which the animals burrowed. Excavations were not carried out beyond a depth of 10 in. as few species penetrate farther, and the tendency for the sides of the hole to collapse detracted from the accuracy of the results. The sand was passed through a series of three sieves of perforated zinc to facilitate collection, the sizes of the holes being 5, 2 and 1 mm. respectively. Two to four squares were dug at each station and the numbers of animals per square metre estimated. A general list of the fauna is given in Appendix 1.

3. METHODS OF MEASURING ENVIRONMENTAL FACTORS

(*a*) *Hydrogen-ion concentration*

The *p*H determination was carried out as soon as sufficient water had drained into the hole so that its exposure to the air would be as short as possible. 10 c.c. of water were transferred to a test-tube to which 5 drops of 0·02 % cresol red were added and the resultant colour was compared with a series of McClendon's buffer solutions.

(*b*) *Salinity*

The samples of water were taken as near as possible to the time of low tide on all occasions. The method used in the salinity determination was that described by Harvey (1928).

(*c*) *Depth of the water-table*

After each hole had been excavated, the distance from the surface of the sand to the level of the water which had accumulated at the bottom was noted. This was done on all occasions at the time of low tide.

(*d*) *Consistency of the sand*

In determining the consistency, the particles of sand were separated into their various sizes by means of a series of sieves and the percentage of each grade was calculated. The grades were named according to Allen (1899). Grade 1, i.e. material left on the 1·5 mm. sieve, was omitted in arriving at the percentage consistency. In nearly all cases it was found that fine sand, i.e. material which passes the 0·5 mm. sieve and when stirred up settles in 1 min., constituted almost the whole of each sample.

4. CULLERCOATS HARBOUR

Cullercoats Harbour lies about $1\frac{1}{2}$ miles to the north of the mouth of the River Tyne. The two breakwaters enclose, at low spring tide, a well-sheltered stretch of sand, roughly 400 yd. long and 120 yd. broad, which slopes gently from the foot of the cliffs to the sea. In November 1930 a series of nine stations was taken at intervals of 12 yd. up the beach near the north end of the harbour, with the object of ascertaining the distribution of the fauna. Station A lay about 6 yd. above the L.W.M. of an average spring tide, Station B lay just below the L.W.M. of neap tides, Station H was near H.W.M. of neap tides, while Station I, the last, was situated just above the H.W.M. of neap tides. The sand was firm and clean, containing very little shell or vegetable debris. Four squares were dug at each station (Table 1).

Scolecolepis girardi was very common in the area between the L.W.M. of spring tides and that of neap tides. A big drop in numbers was experienced at Station C, and from Station D to Station G only

individuals were obtained. This species was usually found at depths from 2 to 6 in. *Nerine cirratulus* occurred in a well-defined zone from Station C to Station G. The numbers dropped suddenly from Station D to Station C, but fell off more evenly to Station G. They were found from 5 in. to 9 in. in depth. Although the results for *Arenicola marina* showed an increase from Station A to Station G, observations of the number of castings on the surface showed that the region of maximum density varied considerably from time to time. At Stations E, F and G about half the worms obtained were of small size, ranging from $\frac{3}{4}$ to $1\frac{1}{2}$ in., the others being comparatively large.

Table 1. *Distribution of the fauna in Cullercoats Harbour, November* 1930

	A	B	C	D	E	F	G	H	I
Scolecolepis girardi	104	139	48	1	1	2	1	.	.
Nerine cirratulus	.	.	6	115	96	55	9	.	.
Arenicola marina	1	2	2	1	8	9	16	.	.
Eteone picta	.	1	.	.	.	.	2	2	.
Enchytraeus albidus	48	30	7	.	.	2	6	.	.
Eurydice pulchra	.	.	.	.	.	1	.	5	.

The figures show the number of animals per square metre.

maximum density was still just below the L.W.M. of neap tides. *Nerine cirratulus* was still most abundant at Stations D and E, though its range had extended to just below the L.W.M. of neap tides. *Arenicola marina* was most numerous at Stations A and B, but, as in November, the individual size varied inversely with the number of specimens, those at Station A being all medium to small in size. No great significance can be attached to the figures of the numbers of *Arenicola* obtained, as many burrowed beyond the depth to which sand was removed in these investigations.

No specimens of *Eteone picta* were obtained in the upper part of the beach, as was the case in November, but only from Stations B, C and D. *Enchytraeus albidus* was again present in the three lowest stations, increasing towards the sea. *Phyllodoce maculata* was found in small numbers in the lower part of the beach. A few individuals of *Eurydice pulchra* were again found about three-quarters of the way to H.W.M. A single specimen of *Haustorius arenarius* was found at Station D, but random sievings in the neighbourhood of that station failed to reveal any more.

Table 2. *Distribution of the fauna in Cullercoats Harbour, March* 1931

	A	B	C	D	E	F	G	H	I
Scolecolepis girardi	8	20	5	.	.	.	.	.	.
Nerine cirratulus	1	28	41	140	228	93	13	.	.
Arenicola marina	17	8	1	2	4	2	.	.	.
Eteone picta	.	4	3	4	.	.	.	.	.
Enchytraeus albidus	68	19	7	.	.	.	.	.	.
Phyllodoce maculata	.	3	4	.	1	.	.	.	.
Eurydice pulchra	.	.	.	.	.	2	5	.	.
Haustorius arenarius	.	.	.	1	.	.	.	.	.
*p*H	7·7	7·7	7·7	7·8	7·9	7·9	7·9	7·9	.
Salinity °/₀₀	35·1	35·0	34·8	34·8	34·4	32·3	27·7	24·0	.
D.W.T.S. (in.)	0·5	1	6	8	8	0·5	Surface	Surface	1
% consistency:									
Fine sand	80·1	96·7	93·8	90·0	92·5	95·9	93·5	98·0	94·3
Silt	0·02	0·02	0·02	0·02	0·02	0·01	0·01	0·01	0·004

(1) The figures show the number of animals per square metre.
(2) D.W.T.S. depth of the water table below the surface.

The chief habitat of *Enchytraeus albidus*, which was obtained from 2 to 8 in., was at, or possibly below, L.W.M., but individuals were scattered irregularly throughout the beach, as were the specimens of *Eteone picta*. *Eurydice pulchra* appeared to prefer the upper beach and the top 2 in. of sand.

No animals were found at Station I, as the period of exposure between tides was too long, and during the lowest neap tides this region of the beach remained uncovered for several days.

In March 1931 a second series of investigations was carried out, using the same stations as on the previous occasion. The *p*H and salinity of the interstitial water and the consistency of the sand were determined for each station. Four squares were dug at each station (Table 2).

The number of *Scolecolepis girardi* was much smaller than that obtained in November, but the region of

Table 3. *Number of species at each station at Cullercoats Harbour in November* 1930 *and March* 1931

	A	B	C	D	E	F	G	H	I
November	3	4	5	5	5	6	6	2	.
March	4	6	6	5	3	3	2	.	.

These results in March show a similar zoning in the distribution of the three dominant species, *Scolecolepis vulgaris*, *Nerine cirratulus* and *Enchytraeus albidus*, to that indicated in November; and a general increase to seaward in the density of all species. In November, six species were found at Stations F and G, whereas in March there were only three species at Station F and two at Station G, whilst Stations B and C each had six. Table 3 shows the number of species probably existing at each station. In the case of *Eteone*, *Enchytraeus* and *Eurydice* their

range is considered as from the highest to the lowest station at which they are found.

In spite of the paucity of species in the upper part of the beach in March, the total number of individuals of all species on the beach as a whole was no smaller as, in both November and March, the average number per square metre was approximately 90.

In general, the numbers of species and of individuals at Cullercoats Harbour were not large. This may be attributed partly to the fact that the level of the sand varied from time to time, according to the set of the currents, and partly to the shortage of food. Low organic content was indicated by the determination of the consistency of the sand, as the percentage of silt, which consisted largely of disintegrated plant and animal remains, was constantly very small and decreased landwards.

With regard to the chemical factors of the environment, the *p*H values showed a slight decrease in acidity of the interstitial water from L.W.M. to H.W.M. The decrease in salinity from L.W.M. to H.W.M. was accelerated in the upper part of the beach by considerable drainage of fresh water from the cliffs. This land drainage resulted also in the low depth of the water table at the upper stations.

In conclusion, these results indicate that the intertidal fauna is distributed in zones, each of the chief species having a more or less definite, separate and fixed area of maximum density (see Figs. 1 and 2). Stephen (1929*b*, 1930) found a similar zoning of the intertidal fauna on many parts of the Scottish coast.

5. THE BLACK MIDDENS, TYNEMOUTH

The Black Middens is the name given to an area of sand and mud lying on the north bank near the mouth of the River Tyne. At low spring tide these muds are exposed for a distance of about 600 yd., the greatest breadth being about 300 yd. At low neap tide practically the whole area is under water (see sketch-map of the Black Middens). At low tide, the Black Middens is a favourite haunt of sea birds whose faeces must considerably augment the organic matter, and so the nutritive value, of the mud. As this is a well-used bait-hunting area for fishermen, almost every part of the mud will at times have been turned over.

In March 1931, while waiting for the beach to be uncovered by the low spring tides, investigations were made at five scattered places (Stations 1–5) in small, well-sheltered patches of mud, as shown in the sketch. A short description of the mud at each station is as follows:

Stations 1 and 2. The mud was sandy, stiff and, below 2 in. from the surface, almost black.

Station 3. The mud was stiff, black and very clayey,

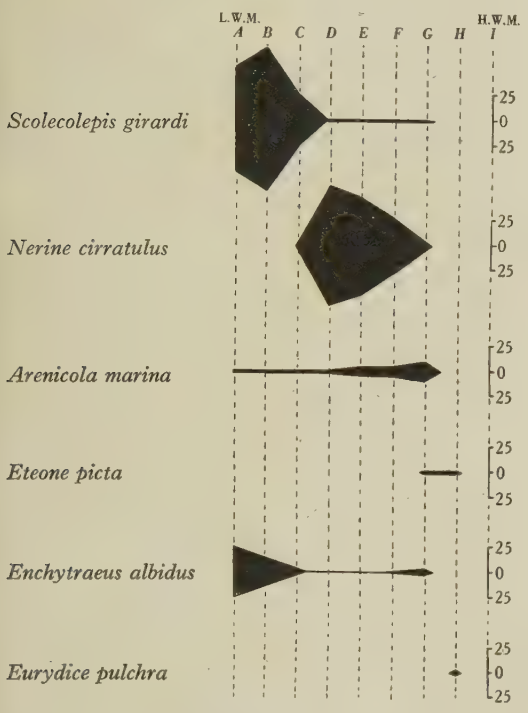


Fig. 1. Cullercoats Harbour, November 1930. Distribution and relative density of the fauna (from Table 1).

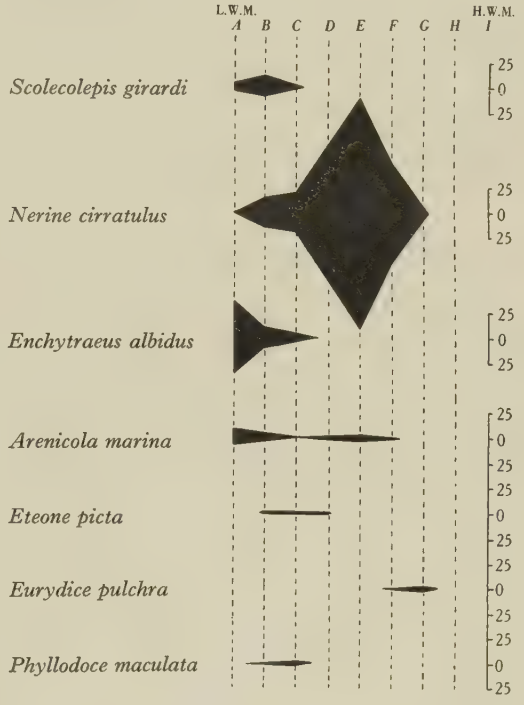


Fig. 2. Cullercoats Harbour, March 1931. Distribution and relative density of the fauna (from Table 2).

containing much fragmentary vegetable matter and having a strong odour. No water drained into the holes that were dug, so the *p*H and the salinity were taken of the water which lay in small pools on the surface, though these values would be of little use in furnishing a clue to the conditions within the sand. A large effluent emptied itself down the cliff adjacent to this position and contributed to the quantity of organic matter in the mud and to the odour.

Station 4. The mud was stiff and clayey, sandier than at Station 3 and rather unstable on the surface. Below a fairly clean layer of about 1½ in. thickness the colour was black. Again no water drained into the hole.

Station 5. Here the sand was firm, fairly clean on top, but very dirty below 1 in. Bedrock was reached at a depth of 1 ft.

Two squares were dug at each station and the numbers of animals per square metre are shown in Table 4.

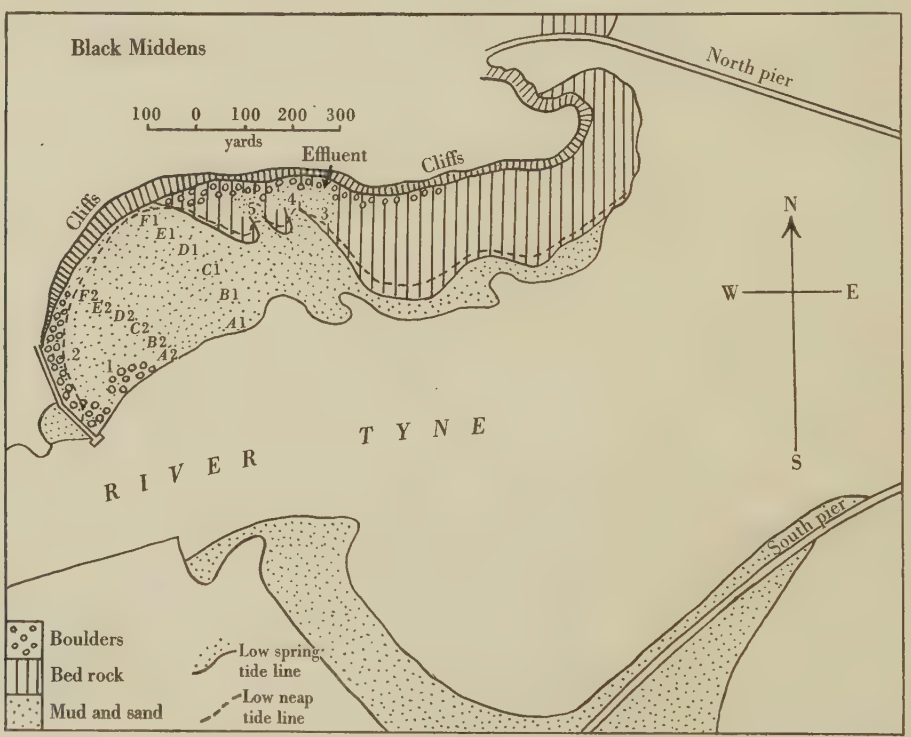
Also in March 1931, a series of six stations (A 1–F 1) was taken from L.W.M. (S.T.) to H.W.M. (N.T.) at the eastern side of the Middens (Table 5), and in April 1931, a second series of six stations (A 2–F 2) was

Table 4. *Distribution of the fauna at the Black Middens, March* 1931

	1	2	3	4	5
Scolecolepis girardi	.	.	104	.	4
Scoloplos armiger	120	56	.	.	.
Nephthys hombergi	46	4	.	.	.
Nereis diversicolor	.	.	.	25	.
Phyllodoce maculata	20	48	.	.	.
Arenicola marina	.	.	.	.	1
Polynoid sp.	1	.	.	.	.
Eteone picta	.	12	.	2	.
Oligochaeta	.	.	520	44	62
Macoma balthica	64	102	4	10	12
*p*H	7·6	7·8	8·2	7·7	7·6
Salinity °/₀₀	30·8	30·9	26·8	31·4	28·9
D.W.T.S. (in.)	4	4	Surface	Surface	4
% consistency:					
Fine sand	96·5	93·7	78·4	86·3	95·3
Silt	1·0	2·0	16·4	11·8	0·6

(1) The figures show the numbers of animals per square metre.

(2) D.W.T.S. depth of the water table below the surface.



Map 1

taken near to the western side (Table 6). By watching the ebbing tide it was possible to fix the stations of the second series at corresponding levels on the beach to those of the first series. For the most part the sand was firm and fairly clean on top, but below an average depth of 4 in. it was almost black. Two squares were dug at each station.

The main differences between the environmental factors obtaining at the Black Middens and those at Cullercoats Harbour were that at the former there existed: (1) A higher degree of shelter from wind and wave action. (2) A greatly reduced slope, resulting in a shorter period of exposure at low spring tide and a complete lack of exposure during neap

tides. (3) A lower average, but greater range of, salinity due to estuarine conditions. (4) Stiff, black mud with much higher organic content, resulting in a higher percentage of silt.

The black colour of the sand was an indication that air did not penetrate far into the sand to oxidize the ferrous sulphide. This condition was most marked at Station 3, where there was a very high percentage of silt (16·4%) and the mud was black to the surface. In these almost anaerobic conditions very few species were found. Only *Scolecolepis girardi* and an Oligochaete were abundant and the two specimens of *Macoma balthica* were only 6 mm. long.

As a result of the fairly constant conditions existing from L.W.M. to H.W.M. at the Black Middens, the different species were more evenly distributed throughout the area. In other words, the restricted zoning found at Cullercoats was less in evidence although it did exist (see Figs. 3, 4).

Table 5. *Distribution of the fauna at the Black Middens, March* 1931

	A1	B1	C1	D1	E1	F1
Scoloplos armiger	152	124	74	64	32	40
Nephthys hombergi	60	58	52	24	14	.
Nereis diversicolor	.	.	.	.	.	10
N. virens	2	2	.	2	.	.
Phyllodoce maculata	14	8	8	34	40	32
Spio filicornis	500	88	32	24	32	.
Arenicola marina	4	4	4	4	4	2
Eteone picta	2	.	.	.	.	8
Oligochaeta	6	8	.	.	.	.
Macoma balthica	4	16	48	50	54	20
Tellina tenuis	8	26	34	38	70	.
Gammarus locusta	.	.	.	.	.	1
*p*H	7·7	7·7	7·9	7·8	7·9	7·9
Salinity °/₀₀	33·2	31·7	31·4	32·3	31·0	31·2
D.W.T.S. (in.)	0·5	4	5	5	6	7
% consistency:						
Fine sand	99·1	98·6	99·1	98·0	98·2	98·1
Silt	0·5	0·4	0·6	0·6	0·6	0·3

(1) The figures show the number of animals per square metre.

(2) D.W.T.S. depth of the water table below the surface.

Thirteen species were obtained in the mud at the Black Middens compared with eight at Cullercoats Harbour. This increase was probably due to the shorter period of exposure between tides. There was also a considerable increase in the number of individuals, only 90 per sq. m. being found at Cullercoats, whereas the density at the Black Middens, taking the average for all stations, was 285 per sq. m. The higher organic content of the mud at the Middens would account for this condition. Finally, as at Cullercoats Harbour, the number of species gradually decreased from L.W.M. to H.W.M. (Tables 7, 8).

With regard to the species inhabiting the mud of the Middens, there was a complete change from the *Nerine-Scolecolepis-Enchytraeus* community of Cullercoats Harbour. *Scolecolepis girardi* was only found in any numbers in the black muds of Station 3. *Scoloplos armiger* was commonly and widely distributed except at Stations 3 and 4, where the percentage of silt was very high, and at Station 5, where the reason for its absence was obscure. Like *Nephthys hombergi*, the numbers of *Scoloplos* increased towards L.W.M., whereas *Phyllodoce maculata* was more numerous towards the land.

Spio filicornis was abundant near the L.W.M. of spring tides, but rapidly dropped off in numbers where the sand was exposed for a longer period. *Nereis diversicolor* showed a decided preference for

Table 6. *Distribution of the fauna at the Black Middens, April* 1931

	A2	B2	C2	D2	E2	F2
Scolecolepis girardi	10	.	.	.	.	.
Scoloplos armiger	114	126	110	76	54	10
Nephthys hombergi	50	42	26	28	10	4
Nereis diversicolor	.	.	.	.	2	16
N. virens	2	2	2	.	2	.
Phyllodoce maculata	8	8	16	12	34	10
Spio filicornis	328	164	50	8	6	.
Arenicola marina	4	6	4	2	4	.
Eteone picta	.	.	.	2	.	.
Oligochaeta	14	.	2	.	.	.
Macoma balthica	6	28	54	40	16	6
Tellina tenuis	4	12	40	62	14	2
Neomysis vulgaris	.	.	.	.	.	1
*p*H	7·7	7·8	7·8	7·8	7·9	7·9
Salinity °/₀₀	33·6	32·4	32·9	31·0	30·5	29·9
D.W.T.S. (in.)	0·5	2	3	5	6	6
% consistency:						
Fine sand	98·0	99·1	98·8	99·4	98·6	98·8
Silt	0·7	0·6	0·5	0·5	0·5	0·4

(1) The figures show the number of animals per square metre.

(2) D.W.T.S. depth of the water table below the surface.

Table 7. *Number of species at each station at the Black Middens in March* 1931

	A1	B1	C1	D1	E1	F1
No. of species	10	10	9	9	8	7

Table 8. *Number of species at each station at the Black Middens in April* 1931

	A2	B2	C2	D2	E2	F2
No. of species	10	9	9	9	9	7

the region near H.W.M. The figures for *N. virens* and *Arenicola marina* are of little significance, as these worms often burrowed beyond the depth of 10 in., to which the digging was restricted, and they were the chief bait sought by the local fishermen.

Gammarus locusta at Station F1 and *Neomysis vulgaris* at Station F2 were merely strays from nearby rock pools.

Two pelecypods, *Macoma balthica* and *Tellina tenuis*, were well distributed, but most thickly in the central and upper stations of the beach. According to their size distribution (see Appendix 2, Tables

18, 19), at Stations A1 and A2 growth was very slow or the span of life was short, as no specimens over 12 mm. (measured from anterior to posterior extremity) were obtained. It appears, judging from the various sizes obtained in the series of Stations A1–F1, that the central region of the beach was the optimum one for both species. In each case Station C1 had the greatest numbers of the largest specimens.

However, in the series of Stations A2–F2, the argest specimens of *Macoma* were at Stations B2 and C2, while those of *Tellina* were at Stations C2, D2 and E2. This was probably a truer indication

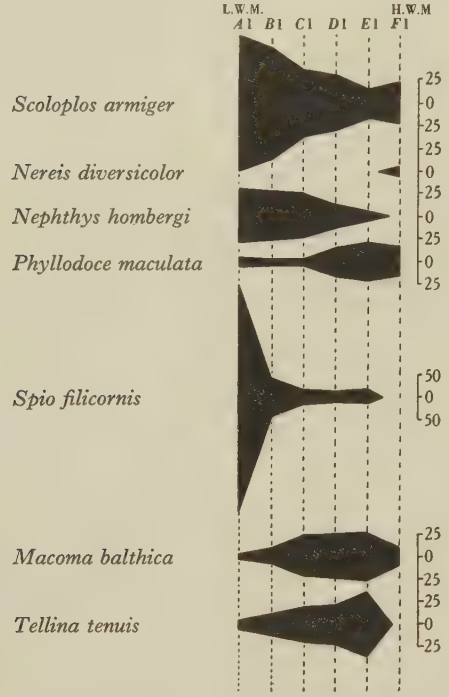


Fig. 3. Black Middens, March 1931. Distribution and relative density of the fauna (from Table 5).

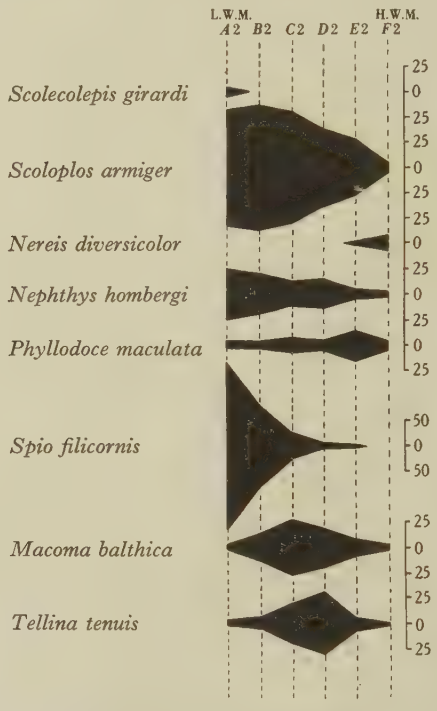


Fig. 4. Black Middens, April 1931. Distribution and relative density of the fauna (from Table 6).

of the size distribution of the two species, as Stephen (1928, 1929*a*) found that, in the Firth of Clyde, *Tellina* grew more rapidly at the landward end of its range. The results for *Macoma* at the Black Middens suggest that it grew more quickly at the seaward end. Stephen (1928, 1929*a*) usually found *Tellina* in greatest numbers near L.W.M. The reversal of this distribution at the Black Middens may be accounted for by the huge numbers of *Spio filicornis* inhabiting the region near L.W.M., occupying the same stratum as *Tellina* and feeding on the same material.

6. BUDLE BAY

Budle Bay, which lies about 3 miles south of Holy Island, is about 2 miles long and 1½ miles broad, and at low tide it is left entirely uncovered by the sea as a stretch of muddy sand. Two large fresh-water streams cross the mud-flats at low tide. The mouth of the bay is blocked, except at the outlet of the main stream, by a narrow sand-spit which is only covered by the highest spring tides. *Zostera* grows over large areas of the inner half of the bay, and beds of mussels cover the muds towards the centre. Numerous birds feed on the mud-flats, which are not, however, used as a bait-hunting area by fishermen.

In June 1931, one series of eight stations (A–H) was taken from the old Oyster Pond straight across the centre of the bay and a second series of four stations (I–L) was taken from Station E to the sand-spit (see sketch-map of Budle Bay). Investigations were not carried on over the inner half of the bay, as the muds in that region were too unstable.

A brief description of the sand at each station is as follows:

1st series

Station A. About 16 yd. from H.W.M. Sand firm, fairly clean on top, but very dark below a depth of 3 in. Large amount of vegetable and shell debris below 3 in.

Station B. Sand firm, black below 3 in. Fair amount of vegetable and shell debris below 7 in.

Station C. Sand firm, almost black below 2 in. Large amount of vegetable matter. Water standing in small pools on the surface.

Station D. Sand firm and clayey, black below 2 in.

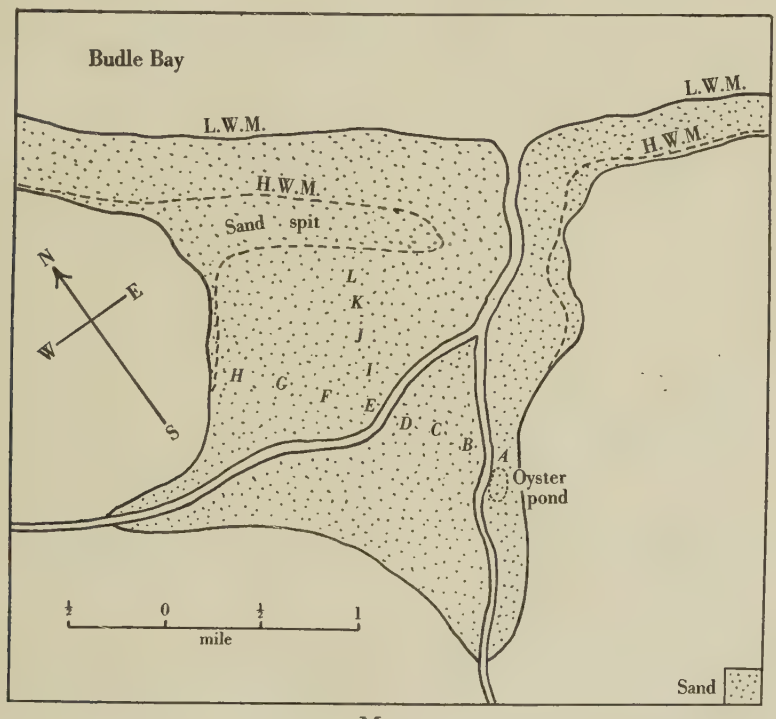
Vast quantity of shell debris, coarse to very fine, and a fair amount of vegetable matter below 7 in.

Station E. Sand very unstable and fairly clean for the top 3 in., but below that depth it was very firm, clayey and black. Fair amount of shell debris, but only a little vegetable matter, below 7 in. This was the lowest-lying station.

Station F. Sand firm and almost black below 1½ in. Large amount of vegetable and shell debris.

Station G. Sand firm and almost black below ¼ in. Fair amount of shell and vegetable debris. Water standing in small pools on the surface.

Station H. About 60 yd. from H.W.M. Sand firm and almost black below ¼ in. Small amount of shell debris and very little vegetable matter.



Map 2

2nd series

Station I. Sand firm and very dark below 1½ in. Fair amount of shell and vegetable debris.

Station J. Similar to Station I, but water standing in small pools on the surface.

Station K. Sand firm and fairly clean throughout. Large amount of shell debris but practically no vegetable fragments.

Station L. Similar to Station K. This station was higher than Station H and was barely, if at all, covered by high neap tides.

By watching the incoming tide gradually cover the mud, it was possible to obtain a rough idea of the relative levels of the stations. These are indicated below the sketch-map of Budle Bay.

Two squares were dug at each station. In Tables 9 and 10 the numbers of animals per square metre are recorded. The results for Station E are repeated in Table 10 to complete the series.

Scoloplos armiger and *Macoma balthica* were by far the commonest animals collected. *Scoloplos* was usually found at depths ranging from 2 to 6 in., while the stratum for *Macoma* was from 1 to 4 in. At first glance their distribution appears very erratic, but a closer consideration reveals an apparent relationship between the two species. The numbers of the one varied inversely with those of the other. This is most strikingly seen when the graphs of the distributions are compared (see Figs. 5, 6). Both species were abundant at Station A. Evidently the conditions prevalent there were exceptionally favourable for both species.

As Hunt (1925) and Blegvad (1914) point out, both animals feed on the same material—the surface layer of mud and detritus in which they live—*Scoloplos* by means of an extrusible gullet, *Macoma* by means of its long, flexible siphons. Because of the nature of its feeding mechanism, *Macoma* undoubtedly draws in also a fair proportion of suspended detrital and planktonic material, with the result that it is less liable to suffer from competition with other detritus feeders, which are unable to take advantage of this alternative source of food.

This competition for food is probably the cause of the relationship between the distributions of the

two species and, possibly on account of its secondary source of supply, *Macoma* appears to be the dominant species, *Scoloplos* being really abundant only when the former is relatively few in numbers.

Table 9. *Distribution of the fauna at Budle Bay, June* 1931

	A	B	C	D	E	F	G	H
Scoloplos armiger	608	224	380	104	584	32	400	.
Nephthys hombergi	.	.	2	.	2	.	.	.
Nereis pelagica	.	.	.	2	12	.	.	.
Nerine foliosa	.	.	.	2	.	.	.	.
Arenicola marina	32	12	8	32	40	12	20	16
Oligochaeta	.	150	32	8	8	6	8	8
Nemertea	.	4	4	10	.	2	.	.
Cardium edule	.	52	88	64	24	156	.	.
Macoma balthica	152	180	96	152	12	152	80	152
Tellina tenuis	.	.	4	8	4	.	.	.
Corophium volutator	.	36	.	68	4	120	.	.
*p*H	7·7	7·9	7·8	7·9	7·8	7·9	8·0	7·8
Salinity °/₀₀	29·7	32·4	32·2	33·4	31·9	33·6	33·2	28·1
D.W.T.S. (in.)	8	1	Sur-face	2	3	3	Sur-face	1
% consistency:								
Fine sand	97·1	93·8	97·3	89·3	94·8	98·5	98·7	95·6
Silt	1·3	3·8	1·3	4·1	0·4	0·8	0·6	0·3

(1) The figures show the number of animals per square metre.
(2) D.W.T.S. depth of the water table below the surface.

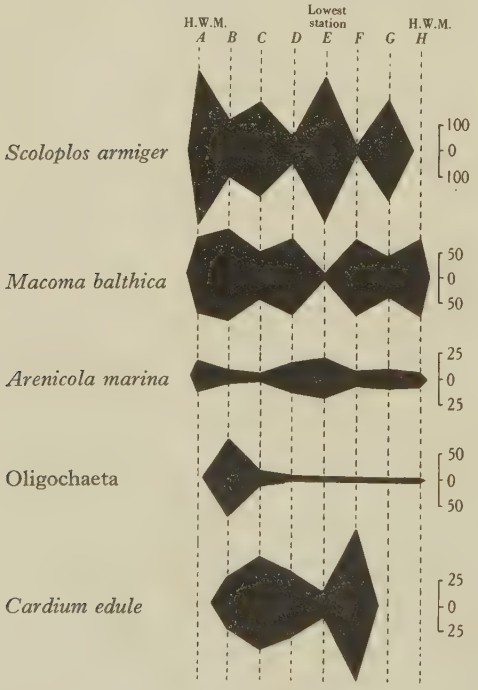


Fig. 5. Budle Bay, June 1931. Distribution and relative density of the fauna (from Table 9).

It will be seen that *Macoma* generally occurred to the extent of 150 per sq. m., but at Stations C, E, G and J the numbers dropped considerably. At Station E, where the biggest drop occurred, the upper 3 in. of sand were very unstable, whereas *Macoma*, like other pelecypods, prefers firmer sand in which it can hold itself in the most advantageous position for the extrusion of the siphons to the surface. *Cardium edule* was also few in numbers here.

Table 10. *Distribution of the fauna at Budle Bay, June* 1931

	E	I	J	K	L
Scoloplos armiger	584	80	24	.	.
Nephthys hombergi	2	.	.	.	.
Nereis pelagica	12	.	.	2	.
Arenicola marina	40	32	32	24	.
Travesia forbesii	.	32	.	.	.
Ophelia limacina	.	.	24	4	.
Oligochaeta	8	.	.	.	.
Cardium edule	24	20	36	12	.
Macoma balthica	12	156	28	20	2
Tellina tenuis	4	32	12	2	.
Corophium volutator	4	.	.	.	.
*p*H	7·8	8·0	7·9	7·8	7·8
Salinity °/₀₀	31·9	32·9	35·2	38·1	39·4
D.W.T.S. (in.)	3	3	Surface	1	0·5
% consistency:					
Fine sand	94·8	99·0	98·9	98·1	98·8
Silt	0·4	0·4	0·2	0·2	0·09

(1) The figures show the number of animals per square metre.
(2) D.W.T.S. depth of the water table below the surface.

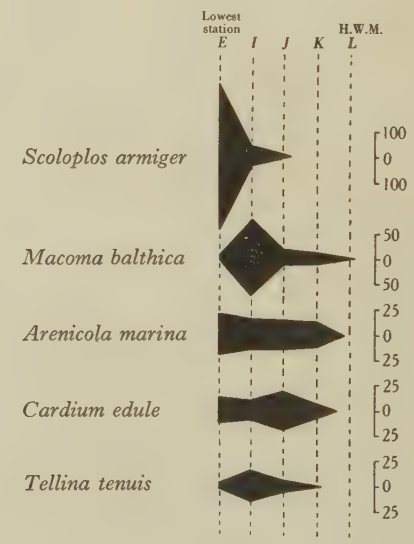


Fig. 6. Budle Bay, June 1931. Distribution and relative density of the fauna (from Table 10).

At Stations C, G and J the sand was very wet, numerous small pools almost covering the surface, and this condition, perhaps by hindering the access of air to the sand, may have been the cause of the reduction in numbers of *Macoma*. Though reduced aeration may interfere with the maximum development of *Macoma*, that it is not entirely deleterious is

proved by the fact that *Macoma* is also an inhabitant of sublittoral muds.

At Stations C, E and G there was a well-marked increase in the numbers of *Scoloplos*, especially at Station E, where *Macoma* was so scarce. At Stations B, D, F, H and I, where *Macoma* was most numerous, considerable reductions in the numbers of the worm occurred.

The complete absence of *Scoloplos* at Station H and the great drop in its numbers at Station I were probably not due entirely to the abundance of *Macoma* but also to the fact that these stations were approximately at the normal limit of the range of the species. At Stations J, K and L the unusually high salinity brought about by evaporation and lack of land drainage, the purity of the sand, the very small organic content and the long period of exposure will all have contributed to cause the scarcity or absence of *Scoloplos*.

Another possible contributory factor to the erratic distribution of *Scoloplos* is indicated by the sand analysis as, except at Station F, there appears to be some correlation between the numbers of the worm encountered and the amount of silt in the sand. Where the percentage of silt is comparatively high, at Stations B and D, there are fewer worms, whereas their numbers are greatest at Stations A, C, E and G, where the proportion of silt is smaller. This was also noticeable at Stations 3 and 4 at the Black Middens, where the percentage of silt was exceptionally high and no specimens of *Scoloplos* were found.

However, with regard to the distribution of *Scoloplos* and *Macoma*, it is surmised that: (1) in the absence of one of these species from Budle Bay the other would be more widely and abundantly distributed; (2) the main cause of the fluctuations is the biological environment; and (3) it is an example of a struggle for food between two species in which the physico-chemical environment gives at one place the advantage to the one species and at another place to the other.

Arenicola marina was well distributed over almost the whole area investigated, varying in numbers from 8 to 40 per sq. m. It is noteworthy that Ashworth (1904) mentions that on Holy Island sands the numbers of *Arenicola* varied from 8 to 42 per sq. yd. An oligochaete was abundant at Station B below a depth of 3 in., but none was obtained just across the stream at Station A. A few individuals of *Nephthys hombergi*, *Nereis pelagica* and *Nerine foliosa* were found at the three lowest lying stations, i.e. C, D and E. Station I was the only place in the bay where *Travisia forbesii* was discovered. The specimens of *Ophelia limacina* obtained at Stations J and K were only $\frac{1}{2}$ in. in length. As no larger individuals appeared to exist, this may have been only a temporary appearance of this species. *Corophium volutator* was absent or scarce where there were surface pools and where the sand was unstable.

Cardium edule was quite common, except near H.W.M., in the upper inch or so of sand. Evidently at Stations C and F they found the most favourable conditions as, for example, remoteness from currents, the optimum period of exposure, and possibly the beneficial effect of fresh water. There seems to be no reason for the absence of cockles at Station G except that lack of aeration was indicated by the black layer of sand extending almost to the surface. The falling off in numbers of *Cardium* at Station E may be attributed to the instability of the sand and also to the fact that this is the lowest lying station where the action of the ebbing and flowing tides may have been strong enough to wash out the smaller cockles or smother them by deposition of sand (Wright, 1926). No specimens less than 12 mm. in length were found at this station.

A third pelecypod found at Budle Bay was *Tellina tenuis*, inhabiting a stratum 1–4 in. in depth, but by no means common. As will be seen from Table 11, the greatest variety of species was found at the two lowest lying stations, D and E, in the central region of the bay, the numbers decreasing towards H.W.M. on the three sides.

Table 11. *Number of species at each station at Budle Bay in June* 1931

	A	B	C	D	E	F	G	H
No. of species	3	7	9	11	10	7	4	3
	E	I	J	K	L			
No. of species	10	7	7	6	1			

With regard to the salinity of the interstitial water, the low figures obtained at Stations A and H were due to land drainage. The high salinities of the stations approaching the sand-spit resulted from evaporation and lack of land drainage. The paucity of species obtained at Station A, where the level of the water table was 8 in. below the surface, was probably due to the excessive drying out.

In June 1932, samples were again taken at Budle Bay, using similar stations to those of the previous year. On account of the very limited time available on this occasion, the *p*H, salinity and consistency were not investigated. Two squares were dug at each station. The results are recorded in Tables 12 and 13.

The general distribution of the commoner species was very similar to that shown the previous year. Again, as will be seen from Figs. 7 and 8, there was a distinct tendency for *Scoloplos* to be most numerous only where *Macoma* was comparatively scarce, i.e. at Stations C, G and J. Taking all stations into consideration, fewer specimens of *Scoloplos* were obtained than in 1931 (cf. 878 in 1932, 1218 in 1931, i.e. a decrease of 27·9%), while there was an increase in the numbers of *Macoma* (cf. 871 in 1932, 591 in 1931, i.e. an increase of 47·4%). Ignoring the additional size group at 3 mm. which was not in evidence in 1931, the percentage increase arrived at for *Macoma* is 27·7%. Thus, the 27·9% decrease of

Scoloplos was counterbalanced by a 27·7 % increase of *Macoma*.

These figures are possibly a coincidence but they definitely suggest that further investigation into the interrelationship between these two animals would probably throw much light on the factors determining the distribution of the littoral fauna.

Table 12. *Distribution of the fauna at Budle Bay, June* 1932

	A	B	C	D	E	F	G	H
Scoloplos armiger	100	106	288	20	12	180	344	86
Nephthys hombergi	.	.	2	.	.	.	.	.
Nereis pelagica	.	.	4	.	2	.	.	.
Nerine foliosa	.	.	2	2	.	.	.	.
Arenicola marina	30	26	20	20	36	54	50	60
Phyllodoce sp.	.	.	.	.	2	.	.	.
Lanice conchilega	.	.	.	2	.	.	.	.
Oligochaeta	2	260	.	.	.	.	.	.
Nemertea	.	.	.	2	.	.	.	.
Cardium edule	2	48	44	28	18	192	24	.
Macoma balthica	90	156	56	40	20	416	58	554
Tellina tenuis	.	.	.	.	4	4	.	.
Corophium volutator	.	210	620	1200	.	.	.	.
D.W.T.S. (in.)	7	1	4	3	3	3	1	0·5

(1) The figures show the number of animals per square metre.
(2) D.W.T.S. depth of the water table below the surface.

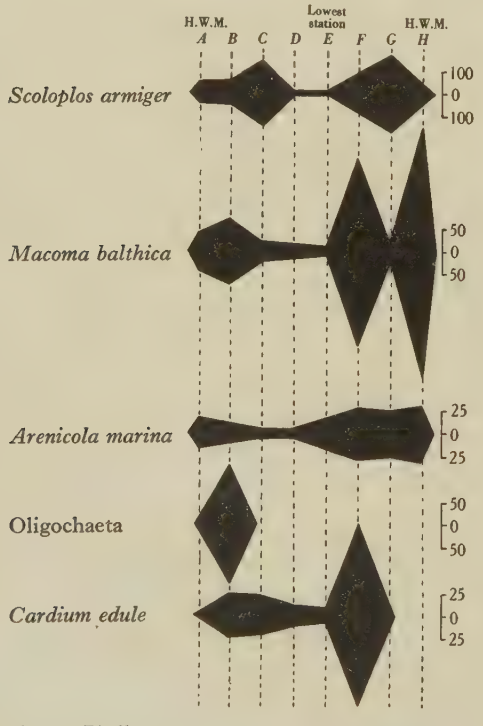


Fig. 7. Budle Bay, June 1932. Distribution and relative density of the fauna (from Table 12).

In 1932 the distribution of *Cardium edule* was almost identical with that found in the previous year, as will be seen by comparing Figs. 5 and 6 with Figs. 7 and 8. Like *Macoma balthica* it was scarce at Station E and then increased in the three directions to a zone of maximum density about half-way to the H.W.M. In both years the average density per square metre was 22.

Station B was again the only station where the oligochaete was numerous.

Corophium volutator was discovered in considerably greater numbers than in 1931, especially at Stations C and D. Unlike other inhabitants of the mud at Budle Bay, this amphipod neither showed preference for any particular zone nor was it distributed throughout the greater part of the bay. No doubt, as Hart (1930) concluded that *Corophium volutator* has an annual or semi-annual life cycle, its numbers fluctuate from year to year according to the favourableness of the breeding conditions.

Table 13. *Distribution of the fauna at Budle Bay, June* 1932

	E	I	J	K	L
Scoloplos armiger	12	140	440	40	.
Nereis pelagica	2	.	.	2	.
Arenicola marina	36	60	32	40	10
Phyllodoce sp.	2	.	.	.	.
Nemertea	.	16	.	.	.
Cardium edule	18	24	32	32	.
Macoma balthica	20	216	68	64	4
Tellina tenuis	4	4	12	8	.
D.W.T.S. (in.)	3	2	Surface	Surface	2

(1) The figures show the number of animals per square metre.
(2) D.W.T.S. depth of the water table below the surface.

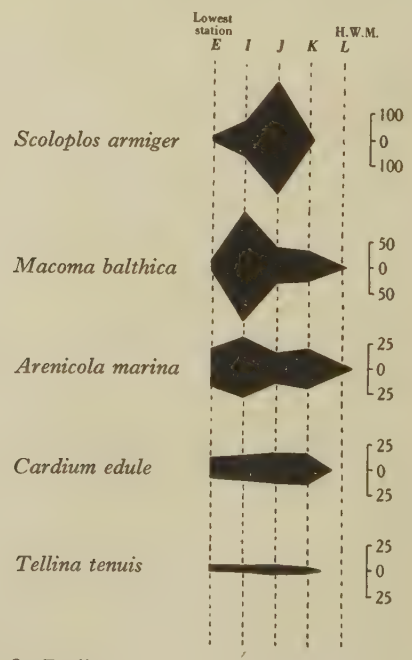


Fig. 8. Budle Bay, June 1932. Distribution and relative density of the fauna (from Table 13).

As in 1931, the number of species at Budle Bay increased towards the lower levels; but, although Station E was the lowest, it had fewer species and individuals than either Station C or Station D, as will be seen from Table 14. This may be accounted for by its proximity to the fresh-water stream, resulting in a range of salinity unfavourable to the full development of the fauna.

Table 14. *Number of species at each station at Budle Bay in June* 1932

	A	B	C	D	E	F	G	H
No. of species	5	6	8	9	7	5	4	3
	E	I	J	K	L			
No. of species	7	7	6	6	2			

In 1931, the average number of individuals per square metre obtained at the twelve stations, A–L, was 392·7. This does not include the numbers of *Corophium*, the only arthropod met with, because, as has already been pointed out, its distribution was so irregular. In 1932, again omitting *Corophium*, the average number of individuals per square metre was 392·5. These remarkably constant figures correspond to the results obtained at Cullercoats Harbour, where the average density of the fauna in March 1931 was almost identical with that found in November 1930.

Thus, although these figures do not take into consideration size or weight, it appears that the population of a beach can be maintained at a constant density from year to year, determined largely, no doubt, by the available food supply. Further work on this subject, carried out over a period of years, should prove interesting.

7. SIZE OF PELECYPODS AT BUDLE BAY

(*a*) *Macoma balthica*

The size distribution of *Macoma* at the Black Middens indicated that it grew more rapidly, or lived longer, and so attained greater size, towards the lower or seaward part of its range. This conclusion was borne out at Budle Bay, where, in June 1931, the largest specimens were dug up at Station E, the lowest, and the next largest at Stations C and F (see Appendix 2, Tables 21, 23) and in June 1932, the largest were found only at Stations C and E (see Appendix 2, Tables 25, 27).

In most cases it was impossible to distinguish the 'winter rings' from the other numerous, concentric rings of growth on the shells, and thus these were of little value in assessing the ages of the *Macomas* obtained. Only occasionally were the 'winter rings' sufficiently clear to bear out the following conclusions. In June 1931, the three commonest sizes were 6, 12 and 18 mm. It seems fairly certain that the 6 mm. mode represented the survivors of the 1930 spat, because at Aberlady Bay, Firth of Forth, Stephen (1929*b*), in June 1929, found modes at 6 and 9 mm. which he held to represent the 1928 and 1927 spats respectively.

As Stephen gives no indication of the conditions existing at Aberlady Bay and does not mention any specimens of *Macoma* of greater size than 12 mm., it is assumed that Budle Bay provided a more favourable habitat for *Macoma*, as greater numbers and also larger individuals were obtained; and as a result of more favourable conditions at Budle Bay growth was faster. Consequently, at first sight, it appears that the modes at 6, 12 and 18 mm. represent year groups, i.e. 1930, 1929 and 1928 respectively, and that those at 9 and 15 mm. were individuals of particularly fast growth.

However, it is possible that all the year groups were not present at Budle Bay, but that there was a hiatus of one or more years between the ages of the larger specimens. For instance, in 1931, the 6 mm. specimens were much more numerous at Stations G and H than at Stations A, B and C, and in a year or two they may be completely missing from the south side of the bay (see Appendix 2, Table 21). Thus, it is much more probable that the 12 and 18 mm. specimens, being widespread and numerous, were the representatives of years, not necessarily consecutive, which were marked by particularly favourable spatting conditions.

Bearing in mind that animals of the same age may not be of the same size at all stations (since *Macoma* appears to grow faster at the more lowlying stations), and that the rate of growth will decrease as the animals grow older, it is assumed that the ages and rate of growth of the *Macomas* are as shown in the following table.

Table 15. *Age and rate of growth of* Macoma balthica *at Budle Bay, June* 1931

Size mm.	Age years	Year spatted	Annual rate of growth mm.
6	1	1930	6
12	2	1929	6
16	3	1928	4
18	4	1927	2
19+	5+	1926 or earlier	1

In June 1932, the commonest sizes were again 6, 12 and 18 mm., with an additional mode at 3 mm. which represented the 1932 spat. As in 1931, there was a marked decrease in the number of specimens larger than 18 mm. It appears, therefore, that the death of the average individual occurred at the end of the fourth year.

(*b*) *Cardium edule*

As in the case of *Macoma*, *Cardium* appeared to grow more rapidly at the lower stations. In both 1931 and 1932, in the series of Stations E–L, the largest specimens were found at Station E and the

next largest at Station I (see Appendix 2, Tables 22, 26). In 1931, the majority of cockles ranged in size from 6 to 12 mm. (see Appendix 2, Tables 20, 22). These showed no 'winter rings', but the umbo of each shell was occupied by a smooth, slightly raised cap, which varied in size from 3 to 6 mm. This represented the 'spat shell' of the previous year, i.e. 1930, while the rest of the shell had been built up during the early months of 1931.

Nine individuals, ranging from 21 to 24 mm. in size, had one distinct 'winter ring' and represented the 1929 spat. The 'winter rings' further indicated that the specimens at 30 mm. were spatted in 1928, those at 36 mm. in 1927, and those at 39 mm. in 1926. The 21–24 mm. mode was not represented in the series of stations from E to L.

Wright (1926) mentions that in December shells 10 mm. long are developed from the spat of that year and that they are at least half an inch long by the next June or July. At Budle Bay, half an inch appeared to be the maximum size, in June, of cockles spatted the previous year, and this agrees with

Table 16. *Age and rate of growth of* Cardium edule *at Budle Bay, 1931 and 1932*

Size in June mm.	Age years	Annual rate of growth mm.
11	1	11
21	2	10
30	3	9
36	4	6
39	5	3

Stephen's (1932) findings at Millport on the Scottish coast, where, in 1930, the average size in June of cockles spatted the previous year was 10·8 mm.

In 1932, most cockles again ranged from 6 to 12 mm. in size (see Appendix 2, Tables 24, 26); but five specimens of 2–3 mm. length were also obtained, and these undoubtedly represented an early batch of the 1932 spat. The survivors of the 1930 spat were of two distinct sizes, 18 and 24 mm., but this is not surprising as in 1931 the cockles of the same spat were most numerous at the extremes of their size range, i.e. 67 specimens of about 12 mm., 53 of about 6 mm., and only 35 of about 9 mm. It appears that conditions for spatting in 1930 were not so favourable in the middle of the season as they were at the beginning and the end. As in 1931, other modes were at 30, 36 and 39 mm. and were 3, 4 and 5 years of age respectively. The 'winter rings' were evenly spaced and distinct and there was no evidence of Orton's 'disturbance rings' (Orton, 1926).

Thus at Budle Bay, *Cardium* appears to live for 5 years, though mortality is very high during the second year. The suggested rate of growth for *Cardium* at Budle Bay is shown in Table 16.

8. CONCLUSION

The fauna of the intertidal zone can withstand a considerable range of environmental conditions, but some, e.g. *Nerine cirratulus*, *Phyllodoce maculata*, *Nereis diversicolor* and especially *Haustorius arenarius*, are favoured by a prolonged period of exposure between tides; some, such as *Nerine cirratulus* and again especially *Haustorius arenarius*, thrive best in clean sand. Most species are most numerous in muds with a fairly high organic content, provided that the consistency is not too fine. The period of exposure, the degree of desiccation, the percentage of silt and the organic content of the sand are apparently the main factors which determine the changes in the dominant species of the communities. The variations of *p*H and salinity recorded had little or no obvious correlation with the distribution of the fauna.

A beach can be divided into a series of zones in which the more abundant species usually have their separate regions of maximum density. The period of exposure of the beach is one of the main factors bringing about the zoning of the fauna, but it is suggested, at least in the case of *Macoma balthica* and *Scoloplos armiger* at Budle Bay, that competition for food may play an important part in limiting the full development of each species. Both these species were abundant and widely distributed, but at each station the numbers of *Scoloplos* varied inversely with those of *Macoma* and, in the second year of the investigations, the percentage decrease of the former was about equal to the percentage increase of the latter. Apparently, a fine balance in numbers is maintained between the various inhabitants of a beach in their efforts to exploit to the full the food content of the sand.

As regards the size and age of the pelecypods obtained, *Cardium edule* and *Macoma balthica* appear to grow more rapidly towards L.W.M. At Budle Bay, the normal span of life for *Macoma* is probably 4 years and for *Cardium* probably 5 years. In each case growth falls off rapidly after the second year.

9. SUMMARY

1. This paper deals with the quantitative distribution of the intertidal fauna at various levels of the beach, and with the effect of certain environmental factors on this distribution, at Cullercoats Harbour, the Black Middens at Tynemouth, and at Budle Bay.

2. The more abundant species were usually found to have separate regions of maximum density.

3. This zoning of the fauna is considered to be chiefly due to the period of exposure of the beach between tides and competition for food between the various species.

4. Notes on the size and probable ages of *Macoma balthica* and *Cardium edule* are given.

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APPENDIX 1

List of species obtained during the investigations

Names as in Marine Biological Association, 'Plymouth Marine Fauna,' 2nd ed. 1931, except nos. 4, 12 and 13 (as in Fauvel, P., 1923 and 1927, 'Faune de France,' 5 and 16) and no. 17 (as in Stephenson, J., 1911, Trans. Roy. Soc. Edinb. 48: 59).

1. *Scolecolepis girardi* (Quatrefages).
2. *Nerine cirratulus* (Delle Chiaje).
3. *N. foliosa* (Aud. et M.-Ed.).
4. *Nereis virens* Sars.
5. *N. pelagica* L.
6. *N. diversicolor* O. F. Müller.
7. *Nephthys hombergi* Lamarck.
8. *Scoloplos armiger* (O. F. Müller).
9. *Eteone picta* Quatrefages.
10. *Phyllodoce maculata* (L.).
11. *Spio filicornis* Fabricius.
12. *Travisia forbesii* Johnston.
13. *Ophelia limacina* (Rathke).
14. *Lanice conchilega* (Pallas).
15. *Arenicola marina* (L.).
16. Polynoid sp.
17. *Enchytraeus albidus* (Henle)
18. Oligochaeta.
19. Nemertea.
20. *Cardium edule* L.
21. *Macoma balthica* (L.).
22. *Tellina tenuis* da Costa.
23. *Corophium volutator* (Pallas).
24. *Gammarus locusta* (L.).
25. *Haustorius arenarius* (Slabber).
26. *Eurydice pulchra* Leach.
27. *Neomysis vulgaris* (J. V. Thompson).

APPENDIX 2

Tables showing the size distribution of pelecypods

All measurements are of the distance between the anterior and posterior extremities.

Table 17. *Size distribution of* Macoma balthica *at Stations* 1–5, *the Black Middens, March* 1931

Size mm.	Av. size group mm.	1	2	3	4	5
16·5–19·5	18	3	1	.	.	.
13·5–16·5	15	5	11	.	.	2
10·5–13·5	12	22	33	.	1	3
7·5–10·5	9	2	6	.	1	1
4·5– 7·5	6	.	.	2	3	.

Table 18. *Size distribution of* Macoma balthica *and* Tellina tenuis *at Stations* A1–F1, *the Black Middens, March* 1931

Av. size group mm.	A1	B1	C1	D1	E1	F1
			Macoma balthica			
18	.	.	2	.	.	.
15	.	2	4	2	10	2
12	1	2	6	19	.	6
9	1	4	12	4	17	2
			Tellina tenuis			
18	.	1	7	3	.	.
15	.	8	6	10	14	.
12	3	.	2	.	10	.
9	.	4	2	6	8	.
6	1	.	.	.	3	.

Table 19. *Size distribution of* Macoma balthica *and* Tellina tenuis *at Stations* A2–F2, *the Black Middens, April* 1931

Av. size group mm.	A2	B2	C2	D2	E2	F2
			Macoma balthica			
18	.	4	2	.	.	.
15	.	5	6	4	1	.
12	1	3	11	13	5	2
9	1	2	8	3	2	1
6	1	.	.	.	.	.
			Tellina tenuis			
18	.	.	1	7	4	.
15	.	5	8	8	.	.
12	1	1	8	16	2	.
9	1	.	3	.	.	1
6	.	.	.	.	1	.

Table 20. *Size distribution of* Cardium edule *at Budle Bay, June* 1931

Av. size group mm.	A	B	C	D	E	F	G	H	Total
65	.	.	1	.	.	.	.	.	1
39	.	.	7	.	.	.	.	.	7
36	.	.	.	.	3	.	.	.	3
33	.	.	.	.	.	.	.	.	.
30	.	.	.	6	3	8	.	.	17
27	.	.	.	.	.	.	.	.	.
24	.	.	2	.	.	.	.	.	2
21	.	.	.	.	.	7	.	.	7
18	.	.	.	.	.	.	.	.	.
15	.	.	.	.	.	.	.	.	.
12	.	4	26	6	6	25	.	.	67
9	.	16	6	13	.	.	.	.	35
6	.	6	2	7	.	38	.	.	53

Table 21. *Size distribution of* Macoma balthica *at Budle Bay, June* 1931

Av. size group mm.	A	B	C	D	E	F	G	H	Total
24	.	.	.	.	4	.	.	.	4
21	.	.	34	.	.	13	.	.	47
18	24	51	6	28	.	17	4	.	130
15	26	.	.	.	.	18	.	.	44
12	22	39	3	13	2	13	19	6	117
9	.	.	1	.	.	9	.	.	10
6	4	.	4	35	.	6	17	70	136

Table 22. *Size distribution of* Cardium edule *at Budle Bay, June* 1931

Av. size group mm.	E	I	J	K	L	Total
36	3	.	.	.	.	3
33	.	1	.	.	.	1
30	3	3	2	4	.	12
27	.	.	.	.	.	.
24	.	.	.	.	.	.
21	.	.	.	.	.	.
18	.	.	.	.	.	.
15	.	.	.	.	.	.
12	6	.	2	.	.	8
9	.	.	9	2	.	11
6	.	6	5	.	.	11

Table 23. *Size distribution of* Macoma balthica *at Budle Bay, June* 1931

Av. size group mm.	E	I	J	K	L	Total
24	4	.	.	.	.	4
21	.	.	.	.	.	.
18	.	23	.	.	.	23
15	.	.	.	.	.	.
12	2	51	13	4	1	71
9	.	.	.	6	.	6
6	.	4	1	.	.	5

Table 24. *Size distribution of* Cardium edule *at Budle Bay, June* 1932

Av. size group mm.	A	B	C	D	E	F	G	H	Total
39	.	.	.	1	3	1	.	.	5
36	.	4	7	.	.	.	1	.	12
33	.	.	.	.	.	.	.	.	.
30	.	.	.	.	2	19	.	.	21
27	.	.	.	.	.	.	.	.	.
24	1	15	5	1	2	18	4	.	46
21	.	.	.	.	.	.	.	.	.
18	.	.	.	.	.	9	5	.	14
15	.	.	.	.	.	.	.	.	.
12	.	.	.	3	.	11	.	.	14
9	.	2	2	5	1	22	1	.	33
6	.	3	6	4	1	16	.	.	30
3	.	.	2	.	.	.	1	.	3

Table 25. *Size distribution of* Macoma balthica *at Budle Bay, June* 1932

Av. size group mm.	A	B	C	D	E	F	G	H	Total
21	.	.	3	.	2	.	.	.	5
18	24	48	14	8	3	46	.	.	143
15	.	.	.	3	.	.	5	12	20
12	3	6	5	5	4	143	10	.	176
9	8	3	2	2	1	9	5	.	30
6	4	5	3	2	.	7	9	175	205
3	6	16	1	.	.	3	.	90	116

Table 26 (*continued*)

Av. size group mm.	E	I	J	K	L	Total
21	.	.	.	.	.	.
18	.	.	2	.	.	2
15	.	.	.	.	.	.
12	.	.	.	2	.	2
9	1	2	6	4	.	13
6	1	2	6	4	.	13
3	.	.	2	.	.	2

Table 26. *Size distribution of* Cardium edule *at Budle Bay, June* 1932

Av. size group mm.	E	I	J	K	L	Total
39	3	.	.	.	.	3
36	.	6	.	.	.	6
33	.	.	.	.	.	.
30	2	.	.	2	.	4
27	.	.	.	.	.	.
24	2	2	.	4	.	8

Table 27. *Size distribution of* Macoma balthica *at Budle Bay, June* 1932

Av. size group mm.	E	I	J	K	L	Total
21	2	.	.	.	.	2
18	3	70	.	.	.	73
15	.	10	.	.	.	10
12	4	8	24	15	2	53
9	1	16	8	6	.	31
6	.	4	2	11	.	17

THE RELATION BETWEEN THE NUMBER OF SPECIES AND THE NUMBER OF INDIVIDUALS IN A RANDOM SAMPLE OF AN ANIMAL POPULATION

By R. A. FISHER (*Galton Laboratory*), A. STEVEN CORBET (*British Museum, Natural History*) and C. B. WILLIAMS (*Rothamsted Experimental Station*)

(With 8 Figures in the Text)

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PART 1. RESULTS OBTAINED WITH MALAYAN BUTTERFLIES

By A. Steven Corbet (*British Museum, Natural History*)

It is well known that the distribution of a series of biological measurements usually conforms to one of three types:

(*a*) the binomial distribution, where the frequencies are represented by the successive terms of the binomial $(q+p)^n$;

(*b*) the normal distribution, in which the results are distributed symmetrically about the mean or average value, and which is the special case of (*a*) when p and q are equal;

(*c*) the Poisson series, in which the frequencies are expressed by the series

$$e^{-m}\left(1+m+\frac{m^2}{2!}+\frac{m^3}{3!}+\ldots\right),$$

where m is the mean and e is the exponential base 2·7183.

The usual practice of calculating the arithmetic mean in a set of measurements of a biological nature, such as wing length of a butterfly, assumes a distribution showing no wide departure from normality, although it does not appear that this procedure has been vindicated.

It is the usual experience of collectors of species in a biological group, such as the Rhopalocera, that the species are not equally abundant, even under conditions of considerable uniformity, a majority being comparatively rare while only a few are common. As far as we are aware, no suggestion has been made previously that any mathematical relation exists between the number of individuals and the number of species in a random sample of insects or other animals. Recently, it has been found (Corbet, 1942) that, leaving out of account the commoner species of which no attempt was made to collect all individuals seen, the number of species S of butterflies of which n individual specimens were collected by a single collector in Malaya was given closely by the expression

$$S=C/n^m,$$

where C and m are constants.* When m is unity, as is the case with the Malayan collection, and has since been found to be a condition which obtains with collections of butterflies from Tioman Island and the Mentawi Islands in which the relation between S and n follows the above equation, the number of species of which 1, 2, 3, 4, ... specimens were obtained was very close to a series in harmonic progression. Thus, the series can be written

$$C\,(1+\tfrac{1}{2}+\tfrac{1}{3}+\ldots).$$

Although this relation holds accurately with the rarer species, there is less agreement in the region of the common species; in fact, theoretical considerations preclude an exact relationship here.

Prof. Fisher (see Part 3) has evolved a logarithmic series which expresses accurately the relation between species and individuals in a random sample throughout the whole range of abundance:

$$S=n_1\left(1+\frac{x}{2}+\frac{x^2}{3}+\ldots\right),$$

where S is the total number of species in the sample, n_1 the number of species represented by single specimens, and x is a constant slightly less than unity but approaching this value as the size of the sample is increased.

The total number of individual specimens, N, in the sample at all levels of abundance is given by $N=n_1/(1-x)$ and $N(1-x)/x$ is a constant α independent of the size of the sample. As the size of the sample is increased, n_1 approaches α.

The Fisher series has been established for all the entomological collections tested in which there was

* This equation may be written

$$\log S=\log C+m\log n,$$

so that the plot of the logarithms of S and n is a straight line.

reason to believe that the collecting had been unselective (see Table 1). It is clear that when S and N are known, as is usually the case, the statistics n_1, x and α can be calculated. It is a curious fact that the number of uniques should approach a constant value with increasing size of collection. It is important to ascertain how far this type of distribution of individuals among species holds in other zoological groups, for it would appear that we have here an effective means of testing whether a collection has been made under conditions approaching random sampling or whether some degree of selection has been exercised, a consideration which is often of some importance in faunistic studies.

tinued after 24 specimens had been taken. In such cases, we have the following information:

The total number of species under 25 individuals per species:

$$S_{(1-24)} = n_1\left(1 + \frac{x}{2} + \frac{x^2}{3} + \ldots + \frac{x^{23}}{24}\right).$$

The total number of individuals at frequencies below 25 per species:

$$N_{(1-24)} = n_1\,(1 + x + x^2 + \ldots + x^{23}).$$

Table 2, which gives the results obtained with the Malayan butterflies, is based on these considerations, and shows the very close relation between the observed and the calculated results.

Table 1. *Entomological collections examined showing the relation between the numbers of species and individuals*

	Observations				Calculations			
	Total individuals	No. between 1 and 24	Total species	No. between 1 and 24	x	n_1 calc.	n_1 found	α
Malayan Rhopalocera	—	3306	620	501	0·997	135·05	118	135·47
Rhopalocera from Tioman Island (east coast of Malaya) (Malay collector, 1931)	157	—	41	—	0·887	15·96	19	18·00
Rhopalocera from Mentawi Islands (excluding Hesperiidae) (C. Boden Kloss and N. Smedley, 1924)	1,878	890	135	110	0·983	32·77	37	33·35
Karakorum Rhopalocera (Mme J. Visser-Hooft; *vide* Evans, 1927)	403	195 (1–28)	27	24 (1–28)	0·984	6·42	6	6·52
Mexican Elmidae (Col.) (H. E. Hinton; *vide* Hinton, 1940)	11,798	—	35	—	0·9998	4·72	4	4·72

How far the results obtained with any particular collection can be regarded as representative of the distribution of the same species group in the area in which the collection was made must obviously depend on the uniformity or otherwise of the conditions prevailing when the collection was made and to the extent to which these conditions are representative of the habitat. In an equatorial forest-clad island with no mountain heights above 2000 ft., conditions are very uniform as far as such orders as Leipidoptera are concerned; although even here some allowance must be made for the fact that collections of butterflies made in such regions are usually poor in the crepuscular species. In temperate climates, it is evident that results obtained during one period of the year are usually inapplicable to other seasons or to the year as a whole. It would appear that the results obtained with the moth trap at Harpenden (see Part 2) can be regarded as giving an accurate picture of the distribution frequencies of the phototropic moths in the area, and it is probable that the same is true of the collection of Mexican Elmidae.

With many collectors, and for a variety of reasons, the collecting of common species is discontinued once a certain number of specimens of these are obtained. In the case of the Malayan Rhopalocera cited, collecting of all individuals seen was not con-

Table 2. *Calculated and observed distribution frequencies of butterflies collected in Malaya*

The values in the second column are obtained from the Fisher series given on p. 42, taking $x = 0{\cdot}997$.

n	S (calc.)	S (found)	Deviations
1	135·05	118	17·05
2	67·33	74	−6·77
3	44·75	44	0·75
4	33·46	24	9·46
5	26·69	29	−2·31
6	22·17	22	0·17
7	18·95	20	−1·05
8	16·53	19	−2·47
9	14·65	20	−5·35
10	13·14	15	−1·86
11	11·91	12	−0·09
12	10·89	14	−3·11
13	10·02	6	4·02
14	9·28	12	−2·72
15	8·63	6	2·63
16	8·07	9	−0·93
17	7·57	9	−1·43
18	7·13	6	1·13
19	6·74	10	−3·26
20	6·38	10	−3·62
21	6·06	11	−4·94
22	5·77	5	0·77
23	5·50	3	2·50
24	5·25	3	2·25
			0·82

According to the calculated values, the total species and total individuals at levels between $n=1$ and $n=24$, are 501·92 and 3132·24 respectively. The actual values found for the total species and total individuals between $n=1$ and 24 are 501 and 3306 respectively.

For the above series in Table 2, $\chi^2=19{\cdot}270$, degrees of freedom $=23$, and P is between 0·90 and 0·80, showing the deviations of the observed results from the calculated values are not significant.

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PART 2. RESULTS OBTAINED BY MEANS OF A LIGHT-TRAP AT ROTHAMSTED

By C. B. Williams

This gives an account of the application of Fisher's series (see Part 3 of this paper) for the frequency of occurrence of species of different levels of abundance in a random sample, to collections of nocturnal Lepidoptera made by means of a light-trap at Rothamsted Experimental Station, Harpenden, Herts, England, during the four years 1933–6. The trap and insects caught in it have already been discussed in a series of papers (Williams, 1939, 1940).

It was necessary to choose, from the material collected, groups in which all or nearly all of the specimens had been identified to species. For this certain families of Lepidoptera were most suited, and the discussion below deals with the captures in the Sphingidae, Noctuidae, Arctiidae, Geometridae and a few other related families. In the Geometridae the genus *Eupithecia* was omitted owing to difficulties of identification. Altogether 15,609 individuals belonging to 240 species were captured. The names and details of numbers for each species will be found in Williams (1939, Tables 6–8).

The frequency of species of different abundance

Table 3 shows the frequency distribution of the species for the four years added together. It will be seen that 35 species were represented by a single individual each; that 85 (including the 35 above) were represented by 5 or fewer individuals; 115 by 10 or fewer; and 205 species by 100 or fewer individuals; leaving therefore 35 species with over 100 individuals per species. The highest total of one species was 2349 individuals of *Agrotis exclamationis*. The results up to 50 individuals per species are represented diagrammatically by the vertical lines in Fig. 1A, giving a curve closely resembling a hyperbola.

If, however, the log number of species is plotted against the log number of individuals as in Fig. 2A it will be seen that, while the straight-line distribution expected for a hyperbola holds approximately true for the rarer species, the number of commoner species is distinctly below the hyperbolic expectation and falls rapidly away from it at higher numbers of individuals per species.

Fisher suggests (see Part 3) that the true series is represented not by

$$n_1, \frac{n_1}{2}, \frac{n_1}{3}, \frac{n_1}{4}, \ldots,$$

which would be the hyperbolic series and which would require an infinite number of species and an infinite number of individuals; but by the series

$$n_1 \ldots \frac{n_1 x}{2} \ldots \frac{n_1 x^2}{3} \ldots \frac{n_1 x^3}{4} \ldots,$$

when n_1 is the number of species with 1 individual and x is a number less than 1.

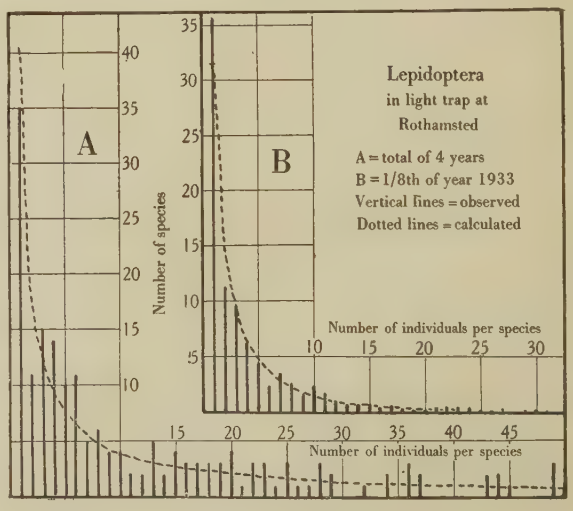


Fig. 1

If this is correct he shows that (1) the total number of individuals (N) is finite and $=\frac{n_1}{1-x}$, (2) the total number of species (S) is finite and

$$=n_1\frac{-\log_e(1-x)}{x}.$$

Table 3. *Observed and calculated captures of Macrolepidoptera in a light-trap at Rothamsted*

No. of individuals per species	(1) All 4 years		(2) Average of single year		(3) Average of ⅛ year		(4) Capsidae, all 4 years	
	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.
1	35	40·14	39·75	37·55	35·63	31·77	18	11·84
2	11	20·03	20·25	18·60	11·38	14·74	8	5·87
3	15	13·32	16·00	12·28	9·63	9·12	3	3·88
4	14	9·96	8·75	9·12	6·24	6·35	4	2·89
5	10	7·95	8·75	7·22	4·50	4·71	2	2·29
	85	91·42	93·50	84·77	67·38	66·68	35	26·77
6	11	6·66	6·25	5·96	2·38	3·64	3	1·89
7	5	5·65	4·25	5·06	3·50	2·90	2	1·61
8	6	4·93	6·00	4·39	2·63	2·55	1	1·40
9	4	4·37	4·00	3·86	1·75	1·93	1	1·23
10	4	3·92	3·50	3·44	2·13	1·62	—	1·10
	30	25·48	24·00	22·70	12·00	12·44	7	7·22
11	2	3·56	2·00	3·10	1·75	1·37	1	0·99
12	2	3·25	2·50	2·81	1·13	1·16	—	0·90
13	5	3·00	2·75	2·57	0·75	0·99	—	0·82
14	2	2·77	2·25	2·36	0·75	0·86	—	0·76
15	4	2·58	3·25	2·19	0·75	0·74	2	0·70
	15	15·16	10·75	13·03	4·18	5·12	3	4·17
16	3	2·42	2·00	2·03	0·50	0·64	—	0·65
17	3	2·27	2·75	1·89	0·63	0·56	—	0·61
18	3	2·14	1·25	1·77	0·38	0·49	—	0·57
19	3	2·02	0·50	1·66	0·25	0·43	—	0·54
20	4	1·92	2·75	1·56	0·25	0·38	—	0·50
	16	10·78	9·25	8·91	2·00	2·53	0	2·87
21	1	1·82	2·75	1·47	0·50	0·34	—	0·48
22	3	1·73	1·75	1·39	0·50	0·30	1	0·45
23	3	1·65	0·75	1·32	0·50	0·27	1	0·43
24	1	1·58	1·00	1·25	0·50	0·24	—	0·41
25	3	1·51	0·50	1·19	0·13	0·21	—	0·38
	11	8·28	6·75	6·62	2·13	1·35	2	2·14
Total to 25	157	151·12	144·25	136·03	87·69	88·12	47	43·17
26	1	1·45	0·25	1·13	0·13	0·19	—	
27	1	1·39	0·25	1·08	0·38	0·17	2	
28	3	1·34	0·75	1·03	—	0·15	—	
29	2	1·29	1·50	0·99	0·13	0·13	—	
30	—	1·24	0·50	0·95	0·25	0·12	—	0·30
	7	6·70	3·25	5·18	0·88	0·76	2	
31	—	1·20	—	0·91	0·13	0·11	—	
32	1	1·16	1·00	0·87	—	0·10	—	
33	—	1·12	1·00	0·83	0·25	0·09	—	
34	2	1·09	0·75	0·80	—	0·08	—	
35	—	1·05	0·25	0·77	—	0·07	—	
	3	5·61	3·00	4·18	0·38	0·51	0	
36	3	1·02	0·75	0·74	0·25	0·06	—	
37	2	0·99	0·25	0·72	0·13	0·06	—	
38	—	0·96	1·00	0·69	—	0·05	—	
39	—	0·93	0·50	0·67	0·13	0·05	1	
40	—	0·91	1·50	0·64	0·25	0·04	—	0·21
	5	4·81	4·00	3·46	0·75	0·26	1	
41	—	0·88	0·75	0·62			—	
42	—	0·86	0·25	0·60			—	
43	2	0·84	0·25	0·58	Total to 40		—	
44	2	0·81	0·25	0·56	89·70	89·65	—	
45	1	0·80	—	0·54			—	
	5	4·19	1·50	2·91			0	
46	—	0·78	0·25	0·53			—	
47	—	0·76	—	0·51			—	
48	—	0·74	1·50	0·50			—	
49	3	0·72	—	0·48			—	
50	—	0·71	—	0·47			—	0·15
	3	3·71	1·75	2·48			0	
Total to 50	180	176·14	157·75	154·24				

Table 3 (*continued*)

Values above 50

(1) Total of 4 years: 51 (4), 52, 53, 54 (2), 57, 58 (2), 60 (3), 61, 64, 67, 73, 76 (2), 78, 84, 89, 96, 99, 109, 112, 120, 122, 129, 135, 141, 148, 149, 151, 154, 177, 181, 187, 190, 199, 211, 221, 226, 235, 239, 244, 246, 282, 305, 306, 333, 464, 560, 572, 589, 604, 743, 823, 2349 = 15,609 individuals of 240 species.

(2) Average of 1 year: 51 (0·75), 52 (0·50), 53 (0·50), 54 (0·25), 58 (0·50), 60 (0·50), 61 (0·25), 64 (0·50), 65 (0·25), 69 (0·25), 73 (0·75), 75 (0·50), 76 (0·25), 77 (0·25), 80 (0·25), 82 (0·25), 83 (0·25), 87 (0·25), 88 (0·50), 90 (0·25), 93 (0·25), 99 (0·50), 100 (0·50), 104 (0·25), 105 (0·50), and the following all (0·25) each: 107, 109, 110, 111, 115, 126, 132, 138, 139, 141, 144, 145, 153, 159, 165, 173, 179, 197, 200, 201, 219, 223, 232, 275, 294, 323, 329, 603, 1799 = 3902 individuals of 176 species.

(3) Average of $\frac{1}{8}$ year: 79 (0·13), 109 (0·13) = 440 individuals of 89·875 species.

(4) Capsidae = 53, 80, 85, 158, 206, 237, 298 = 1414 individuals of 57 species.

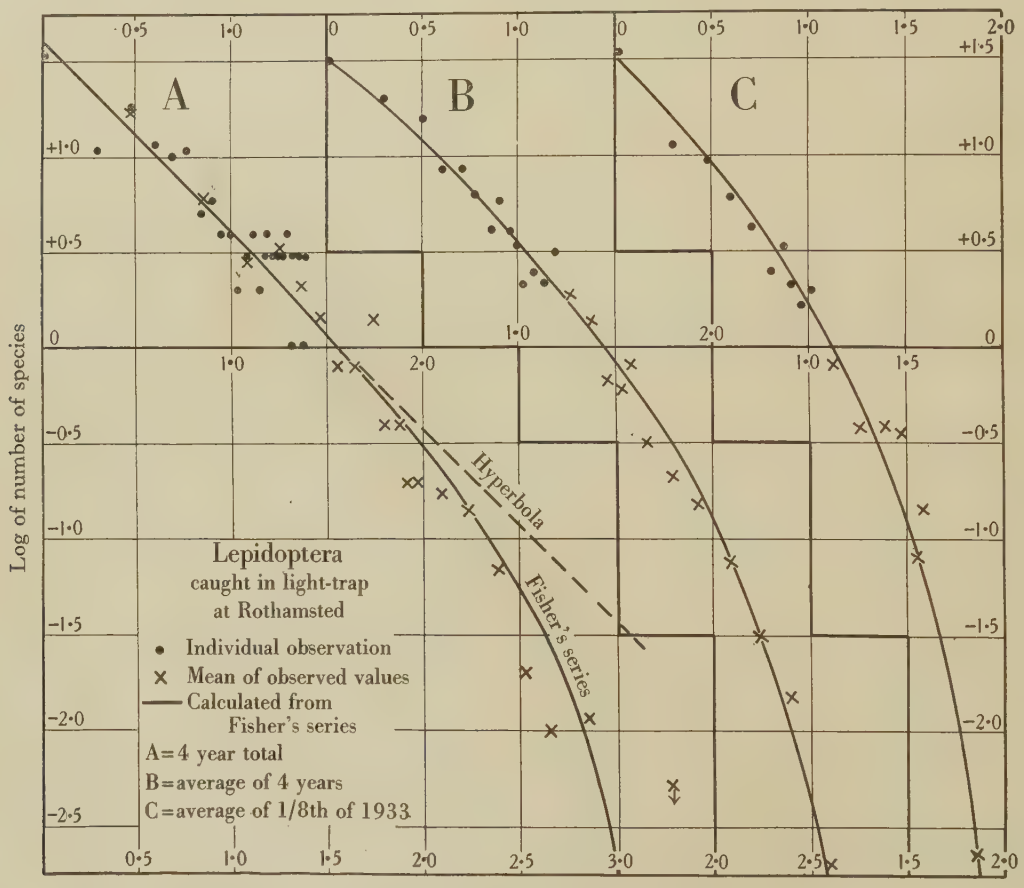


Fig. 2

Thus if N and S are known both n_1 and x can be calculated, and hence the whole series is known.

If N is large n_1 tends to become a constant value α, and Fisher shows that for all levels of sampling for the same population $x = \frac{N}{N+\alpha}$.

Applying these formulae to our Macrolepidoptera with 15,609 individuals of 240 species we find

$$\alpha = 40{\cdot}24,\ n_1 = 40{\cdot}14,\ x = 0{\cdot}997429.$$

The calculated values for n_2, n_3, etc., are shown in Table 3 opposite the observed figures and also by curves in Figs. 1 A and 2 A. In the latter the log of the frequency is plotted against the log of the number of individuals per species.

It will be seen that for both common and rare species the calculated values are very close indeed to the observed. The calculated number of species with one individual is slightly larger (40·14) than the observed (35). By calculation there should be 116·9

species with 10 or fewer individuals and the observed number was 115. The close resemblance at higher frequencies is best seen in Fig. 2A.

If, instead of adding the four years together, we take the average number of individuals in each year and the average number of species with 1, 2, 3, etc., individuals we find the observed results in the trap to be as in the second column of Table 3. There are 3902 individuals of 176 species. Calculations from these figures show that $x=0{\cdot}990356$ and $n_1=37{\cdot}55$. The calculated series is shown up to 50 individuals per species in Table 3 and diagrammatically in Fig. 2B. The calculated n_1 is slightly smaller than the observed.

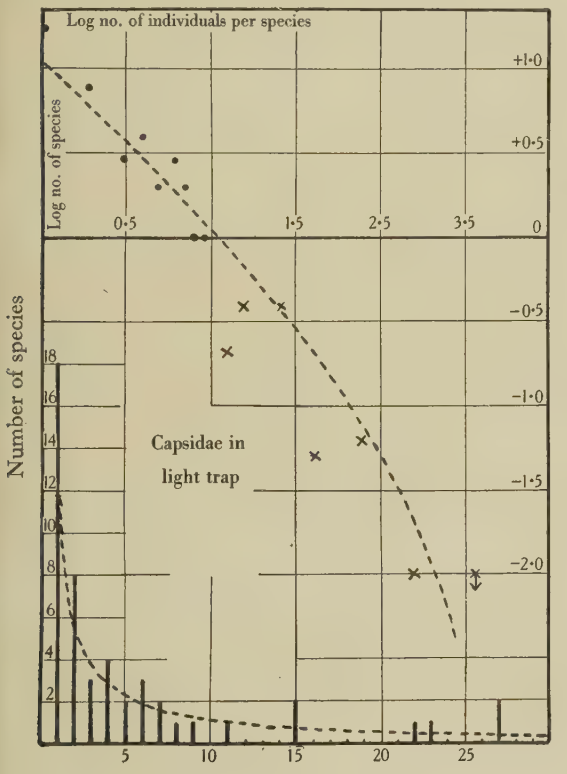


Fig. 3

A still smaller sample was obtained by dividing the catches in the year 1933 into 8 samples, the first including those insects caught in the 1st...9th...17th day, the second on the 2nd...10th...18th day, etc. The average for the 8 samples is shown in the third column of Table 3, together with the calculated figures. The number of individuals was 440, the number of species 89·9, from which $n_1=31{\cdot}77$ and $x=0{\cdot}9278$. The calculated n_1 is slightly smaller than the observed. Results are shown diagrammatically in Figs. 1B and 2C. The close resemblance in both the two series of the observed and calculated results is very striking.

Thus in the Macrolepidoptera caught in the light-trap at Harpenden samples as large as 15,609 individuals and as small as 440 individuals both agree very closely with the results calculated from Fisher's series.

The only other group of insects captured in the light-trap in which the majority of the specimens were identified was the family Capsidae of the Heteroptera. These were identified by D. C. Thomas (1938). In the four years 1414 individuals of 57 species were captured. The observed and calculated results are shown in the fourth column of Table 3 and in Fig. 3. The calculated n_1 is 11·87 and $x=0{\cdot}9916$.

It will be seen that the fit is not so good as in the Lepidoptera. The observed number of species represented by only one individual is 18 and the calculated less than 12. In general there are rather more of the rarer species than the calculated series indicates, and fewer of the commoner species.

Table 4 shows a summary of all the various samples taken from the Lepidoptera and the Capsidae. It will be seen that there is a slight general tendency for the calculated value of n_1 to be below the observed. In the Macrolepidoptera for one or more years this is not so obvious, but it is distinct in the one-eighth year samples. In the Noctuidae only there are four results below and two practically equal to the observed figure; but in the Capsidae there are five below and only one equal. This requires further investigation.

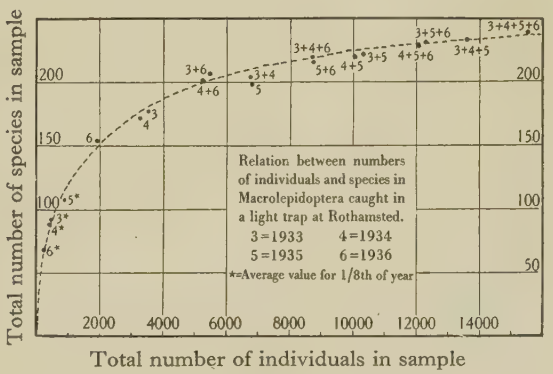


Fig. 4

The relation between the number of species and total number of individuals in the sample

In Tables 4 and 5 are shown a number of samples of different size taken from the light-trap captures with the number of individuals in the sample and the number of species represented.

Fig. 4 shows diagrammatically the number of species in relation to the number of individuals for all the different samples of Lepidoptera. It will be seen that there is a very regular relation between the observed numbers. This form of diagram is, however, not very suitable for showing large samples,

Table 4. *Calculations of x, α and n_1 for various light-trap samples*

	Individuals	Species	x	α	Species with 1 individual: Calc.	Species with 1 individual: Obs.
			Macrolepidoptera			
1933	3,540	178	0·98903	39·15 ± 1·45	38·62	32
1934	3,275	172	0·98834	38·64	38·19	34
1935	6,817	198	0·994425	38·19	37·94	37
1936	1,977	154	0·980595	39·05	38·30	50
4 years: Total	15,609	240	0·997429	40·24 ± 1·06	40·14	35
Average	3,902	176	0·990380	37·90	37·54	39·75
⅛ of 1933	561	105	0·93638	38·12	35·69	38
,,	581	104	0·94028	36·90	34·70	39
,,	458	86	0·93609	32·27	29·27	34
,,	357	84	0·91157	34·63	31·57	41
,,	344	80	0·91306	32·75	29·90	35
,,	282	75	0·8941	33·40	29·86	28
,,	503	101	0·92968	38·05	35·37	38
,,	427	81	0·93725	29·26	27·42	36
Average of 8 × ⅛	440	89·5	0·9278	34·24 ± 2·67	31·77	35·63
			Noctuidae only			
1933	1,636	84	0·9887	18·70 ± 1·02	18·49	18
1934	1,894	73	0·9922	14·89	14·77	14
1935	5,413	94	0·997	16·29	16·23	21
1936	1,362	71	0·9886	15·71	15·53	20
4 years: Total	10,304	112	0·9983	17·56 ± 0·63	17·52	20
Average	2,576	80	0·994	15·55	15·46	18·25
			Capsidae			
1933	341	26	0·981	6·60 ± 0·71	6·5	10
1934	479	38	0·98	9·77	9·6	17
1935	446	24	0·988	5·41	5·45	5
1936	148	23	0·95	7·79	7·40	9
4 years: Total	1,414	57	0·9916	11·98 ± 0·76	11·88	18
Average	354	27·75	0·98047	7·04	6·90	10·25

Table 5. *Number of individuals and species in different sized samples from the light-trap*

	Macrolepidoptera: Indiv.	Macrolepidoptera: Sp.	Noctuidae only: Indiv.	Noctuidae only: Sp.	Capsidae: Indiv.	Capsidae: Sp.
1933	3,540	178	1,636	84	341	26
1934	3,275	172	1,894	73	479	38
1935	6,817	198	5,413	94	446	24
1936	1,977	154	1,362	71	148	23
Average of single year	3,902	176	2,576	80·5	353·5	27·75
1933 + 1934	6,815	204	3,530	94	820	46
1933 + 1935	10,357	222	7,049	106	787	37
1933 + 1936	5,517	206	2,998	95	489	32
1934 + 1935	10,092	220	7,307	100	925	45
1934 + 1936	5,252	200	3,256	88	627	48
1935 + 1936	8,794	216	6,775	101	594	31
Average of years in pairs	7,804	211·3	5,152	97·3	707	39·8
1933 + 1934 + 1935	13,632	234	8,943	109	1,266	52
1933 + 1934 + 1936	8,792	219	4,892	299	968	54
1933 + 1935 + 1936	12,334	232	8,411	109	935	42
1934 + 1935 + 1936	12,069	229	8,669	105	1,073	51
Average of years in threes	11,706	228·5	7,728	105·5	1,060·5	49·75
All 4 years	15,609	240	10,305	112	1,414	57

and in Fig. 5 (heavy line) the same data are shown with the number of individuals in the sample expressed as a logarithm.

According to Fisher's theory, any population should have a constant value of α for samples of any size taken from it under identical conditions. Thus it follows that for any population, if the value of α is obtained from one sample, the values of

$$x\left(=\frac{N}{N+\alpha}\right)$$

and hence of S can be calculated for other samples of different sizes from the same population. In Fig. 5 there are shown as dotted lines typical calculated relations between the number of individuals and number of species for different values of α. It will immediately be seen that the observed values for the Lepidoptera fit very closely to the calculated relation for $\alpha=40$. The slight difference between the observed and calculated figures will be discussed below.

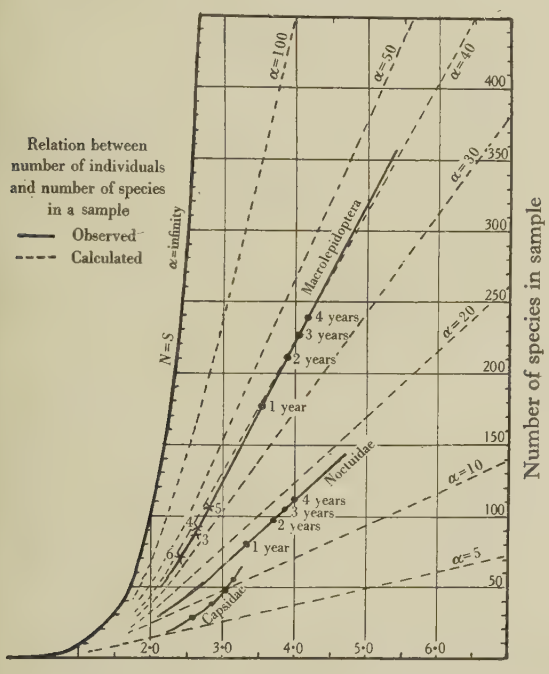


Fig. 5

It will also be seen that the observed values for the Noctuidae alone fit very closely to a value of $\alpha=17{\cdot}5$, but that the observed values for the Capsidae cut rather rapidly across the α lines giving too few species in small samples and too many in large samples (when they are taken, as in the light-trap, in more than one year). The various calculated values of α in the different samples together with their standard deviation as calculated from Fisher's formula are given in Table 4. It is suggested that the parameter α should be known as the 'index of diversity' of the population.

The differences between the observed and calculated values for Lepidoptera and for Capsidae are shown diagrammatically on a larger scale in Fig. 6. In the Lepidoptera (Fig. 6A) it will be seen that more species are obtained in a sample spread over several years than would be expected in a sample of the same size taken in a single year. Thus when a sample of 15,609 (log 4·19) Lepidoptera was captured in four years 240 species were represented. If the same number had been caught in one year it will

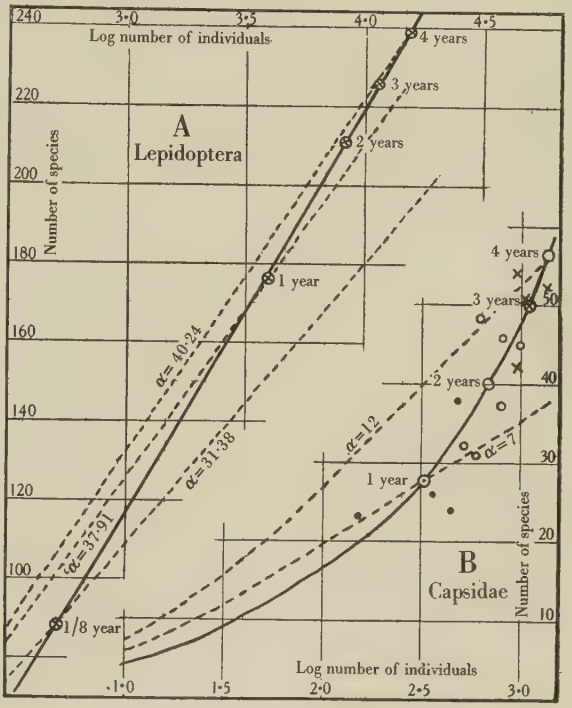


Fig. 6

be seen (by finding where the $\alpha=37{\cdot}91$ line cuts log 4·19) that only about 226 species would have been expected. Otherwise about 14 extra species have been captured owing to the new biological conditions introduced by sampling over a longer period. The same effect on an even larger scale is obvious between samples captured throughout a whole year and those captured in one-eighth of the year. Thus the departure of the observed from the calculated results is immediately explicable by the alteration of conditions introduced by spreading sampling over a longer period of time.

The Capsidae (Fig. 6B) show the same effect in a more extreme form. With 1414 individuals caught in four years 57 species were obtained, whereas if the same-sized sample had been taken in one year we would only have expected about 36 species. There is thus a considerable increase of species by spreading

the catch over a longer period. This is indicated also by a fact that I have already pointed out (Williams, 1939, p. 96) that in the Capsidae 50% of the 57 species occurred only in a single year, as compared with a figure of only 19% in the Macrolepidoptera. The Capsidae fauna therefore is much more variable from year to year than is the Lepidoptera.

Since with high number of N the relation between the number of species and log number of individuals becomes practically a straight line (both theoretically and observationally) it is possible to extrapolate the observed curve for the Macrolepidoptera with some interesting and suggestive results. In the first place it should be noted that the number of British species in the families of Macrolepidoptera dealt with is 681, and the number of species already recorded for Hertfordshire (where the trap was situated) was 461.

Thus in four years we have captured approximately 16,000 individuals representing 240 species. After ten years we would have captured approximately 40,000 individuals which would contain about 275 species. After 50 years the 200,000 individuals would include 340 species. After 100 years the 400,000 would include 365 species or only 25 new species in 50 years.

To get the Hertfordshire fauna (461 species) we would have to collect over three million insects, and this would take, at the present rate, nearly 1000 years. When this level was reached only one new species would be added in 20 years' trapping. To get the British fauna (681 species) we would have to trap about 1800 million insects which would take nearly half a million years!

Doubling the number of insects caught (and hence the time of trapping) at any level, except for very small samples, always adds about 30 species to the total.

These figures are based on the curve allowing for captures of 4000 insects per year. If the whole number were caught in one year (assuming that to be possible) the number of species would be less in each case. So that 400,000 individuals would give 350 species (instead of 368), the Hertfordshire fauna would require 8 million insects, and the British fauna 3200 million.

The seasonal changes of α in the Macrolepidoptera

If the Macrolepidoptera captured in the light-trap during the four years are tabulated month by month the numbers of individuals and species in each month (excluding the five winter months when numbers are too small) are shown in Table 6 together with the approximate value of α. The changes in α are shown in Fig. 7.

There is a regular seasonal change which is almost identical in each year; the value of α rises from a low value in April to a maximum in July and back to a low value in October. There is a very much greater difference between the α values for two different months than there is for the same month in two different years. For example, the number of insects caught in July 1935 was almost seven times as great as the number in July 1936, and yet the values of α are almost identical; but rather more insects in August 1936 than in July gives a considerably smaller value, and an almost identical number of insects in September 1936 gives a value of α only about one-third as great.

There is no doubt whatever that there is a seasonal

Table 6. *Number of individuals and of species of Macrolepidoptera in each of the summer months of the four light-trap years, with the approximate values of α*

	1933			1934			1935			1936		
	N	*S*	α	*N*	*S*	α	*N*	*S*	α	*N*	*S*	α
Apr.	70	12	4·0	55	8	2·5	24	9	5·0	16	5	3·0
May	318	38	11·0	131	27	10·0	119	26	10·0	38	16	10·0
June	693	73	20·5	518	53	14·5	1178	67	15·5	434	45	13·0
July	987	90	24·0	1059	97	25·5	3136	119	24·5	449	68	22·5
Aug.	701	59	15·5	591	51	13·5	1920	84	18·0	491	57	16·5
Sept.	389	30	7·5	528	31	7·0	647	36	8·0	448	33	8·0
Oct.	220	14	3·0	152	14	3·5	171	18	5·0	59	14	5·0

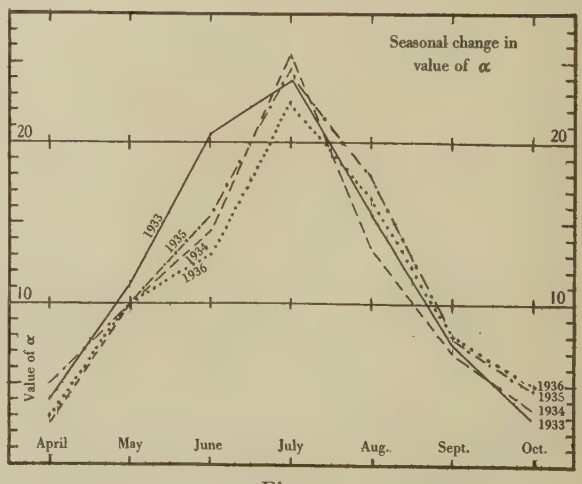


Fig. 7

change in α or in the 'richness of species' quite independent of the seasonal change in numbers of insects.

Value of α for a single night in a month

In the month of July 1935, which was a month of high catches of Lepidoptera in the light-trap, 2,586 Noctuidae were captured, belonging to 56 species. This gives α (for Noctuidae only) = 10·09.

The following were the captures on seven selected nights in the month:

Date	N	log N	S
1	429	2·63	18
6	143	2·16	10
11	394	2·60	18
16	11	1·04	7
21	47	1·67	17
26	64	1·80	11
31	53	1·72	10
	Mean	1·95	13

From these figures $\alpha = 4{\cdot}2$. Thus it is considerably smaller for a short period of sampling than for a longer period. This would be expected, as the variety of species available for catching on a single night must be less than that on a series of different nights.

Comparison of results from two light-traps a short distance apart

During the autumn of 1933 two light-traps were kept running simultaneously from 8 August to 31 October. One was in the fields at Rothamsted (the standard trap used in all the previous calculations) and the other was about 400 yards away on the roof on the Entomology building at a height of about 35 ft. from the ground. This overlooked a more varied environment with gardens and mixed vegetation.

The captures of Noctuidae in the two traps were as follows:

	Field trap		Roof trap	
1933	N	S	N	S
8–31 Aug.	419	26	706	36
Sept.	355	18	593	32
Oct.	155	9	557	19
	929	40	1856	58
	$\alpha = 8{\cdot}51 \pm 0{\cdot}7$		$11{\cdot}38 \pm 0{\cdot}7$	

The difference between the two values of α is 2·8 and the standard error of the difference approximately 1·0, so that difference is probably significant. The roof trap has caught a larger number of individuals but a still larger number of species. This is probably due, as mentioned above, to the considerably more varied vegetation that it overlooked.

The effect on number of species of increasing the size of a sample

Fisher has shown that

$$S = \alpha \log_e \left(1 + \frac{N}{\alpha}\right).$$

If the sample is large so that N is large compared with α we can neglect the 1 in comparison with N/α. Hence for large samples

$$S = \alpha \log_e \frac{N}{\alpha},$$

hence

$$S_{2N} - S_N = \alpha \left(\log_e \frac{2N}{\alpha} - \log_e \frac{N}{\alpha}\right) = \alpha \log_e 2.$$

So the number of species added to a large sample by doubling it is $\alpha \log_e 2x = 0{\cdot}693\alpha$. Similarly, if the sample were increased 10 times the number of new species added $= \alpha \log_e 10 = 2{\cdot}3\alpha$ approximately. On the other hand, if the size of the sample is multiplied by e (= 2·7183) the additional number of species is $\alpha \log_e e$, which is equal to α.

For example, with the Macrolepidoptera in the light-trap α = approximately 40, so doubling a large catch will at any level add approximately 28 new species, multiplying it by 10 will add approximately 92 species.

To add one new species to a large sample $\alpha \log_e z$ must equal 1, when z is the factor by which the sample must be multiplied, i.e.

$$\log_e z = 1/\alpha;$$

for example, if $\alpha = 40$ as in the Macrolepidoptera above

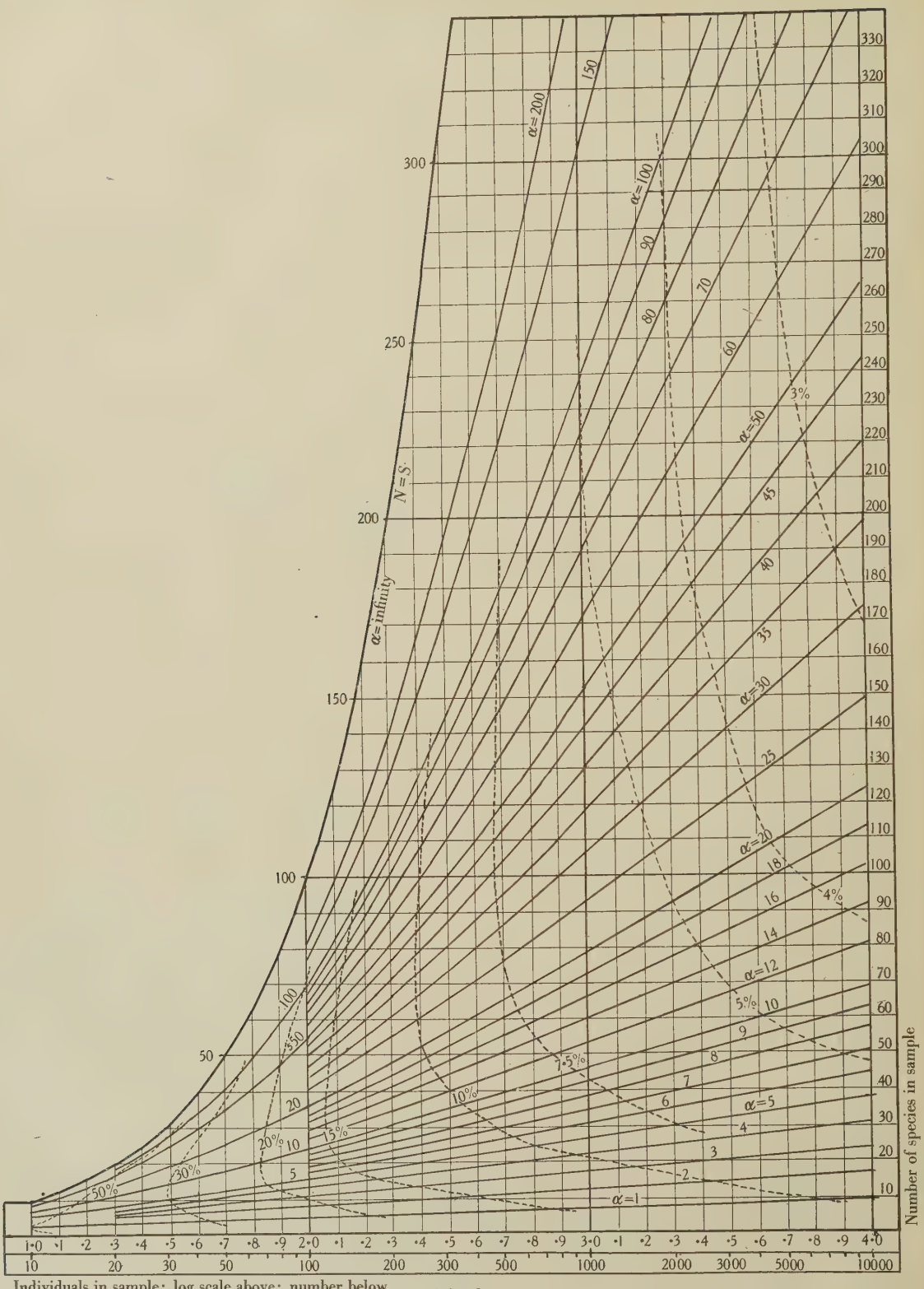
$$\log_e z = 0{\cdot}025, \quad z = 1{\cdot}0255;$$

hence the number of insects must be increased by just over 1/39 of the original sample to add one additional species.

Diagram showing the interrelation of N, S, α and the standard error of α

From the formulae provided by Prof. Fisher α and the error of α can be calculated if N and S are known, and similarly S can be calculated if N and α are known. These calculations can be made to any number of decimal places. For many purposes, however, a close approximation to α and its error is all that is necessary, and if this can be obtained rapidly without calculation so much the better.

For this purpose Fig. 8 has been drawn up. In this the vertical axis is the number of species and the horizontal the log of the number of individuals in the sample. A large number of values of α have been inserted as diagonals, with the result that if any two of these three factors is known the third can be easily estimated. Thus with a sample of 1000 individuals (log = 3·0) containing 60 species $\alpha = 14$. Or with $\alpha = 25$ a sample of 10,000 individuals should


α = 200
150
α = 100
90
80
70
60
3%
α = 50
45
40
35
α = 30
25
α = 20
18
16
4%
14
α = 12
5%
10
9
8
7
6
α = 5
4
3
2
α = 1
N = S
α = infinity
100
50
20
10
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120
110
100
90
80
70
60
50
40
30
20
10
Number of species in sample
1·0 ·1 ·2 ·3 ·4 ·5 ·6 ·7 ·8 ·9 2·0 ·1 ·2 ·3 ·4 ·5 ·6 ·7 ·8 ·9 3·0 ·1 ·2 ·3 ·4 ·5 ·6 ·7 ·8 ·9 4·0
10 20 30 50 100 200 300 500 1000 2000 3000 5000 10000
Individuals in sample: log scale above; number below

Fig. 8

Table 7. *Values of S for different combinations of N and α*

α \ N	10	20	50	100	200	500	1000	2000	5000	10,000	100,000
1	2·40	3·00	3·93	4·62	5·30	6·22	6·91	7·60	8·35	9·21	—
2	3·58	4·80	6·52	7·86	9·23	11·05	12·43	13·82	15·65	17·03	—
3	4·40	6·08	8·62	10·61	12·64	15·37	17·44	19·51	22·26	24·34	—
4	5·01	7·17	10·41	13·03	15·73	19·34	22·10	24·87	28·53	31·30	—
5	5·49	8·04	11·99	15·03	18·57	23·08	26·52	29·97	34·54	38·01	49·57
6	5·89	8·80	13·40	17·23	21·21	26·60	30·73	34·87	40·36	44·51	—
7	6·22	9·45	14·68	19·09	23·71	29·98	34·78	39·61	46·01	50·86	—
8	6·49	10·02	15·85	20·82	26·06	33·08	38·79	44·21	51·51	57·06	—
9	6·72	10·53	16·92	22·45	28·30	36·32	42·47	48·67	56·90	63·14	—
10	6·93	10·98	17·92	23·98	30·45	39·32	46·15	53·03	62·17	69·08	92·10
12	7·27	11·76	19·70	26·80	34·46	45·02	53·21	61·46	72·42	80·72	—
14	7·55	12·45	21·28	29·36	38·21	50·44	59·96	69·57	82·33	92·02	—
15	7·67	12·71	21·99	30·42	39·93	53·03	63·22	73·50	87·18	97·56	—
16	7·76	12·98	22·67	31·70	41·65	55·58	66·16	77·38	91·97	103·02	—
18	7·96	13·45	23·92	33·84	44·89	60·48	72·63	84·76	101·36	113·80	—
20	8·11	13·86	25·06	35·84	47·96	65·16	78·64	92·30	110·52	124·34	170·35
25	8·43	14·70	27·48	40·25	54·93	76·13	92·85	109·87	132·58	149·86	—
30	8·61	15·33	29·43	43·98	60·84	86·16	106·05	126·45	153·66	174·36	—
35	8·82	15·82	31·08	47·25	66·64	95·52	118·55	142·21	173·92	198·07	—
40	8·92	16·24	32·44	50·12	71·68	104·12	130·32	157·28	193·44	221·04	—
45	9·04	16·52	33·62	52·65	76·23	112·23	141·53	172·72	212·36	243·36	—
50	9·12	16·85	34·65	54·95	80·45	119·90	152·25	185·7	230·75	265·15	380·07
60	9·27	17·22	36·36	58·86	87·96	133·98	172·32	212·1	266·04	307·32	—
70	9·35	17·64	37·73	62·16	94·50	146·79	191·03	237·1	299·81	347·83	—
80	9·42	17·84	38·80	64·88	100·24	158·48	208·24	260·6	330·80	386·88	—
90	9·48	18·09	39·78	67·23	105·30	169·20	224·46	283·1	363·15	424·71	—
100	9·53	18·20	40·60	69·31	109·9	179·2	239·8	304·5	392·2	461·5	690·9
150	—	—	—	—	—	219·9	304·2	399·3	530·3	632·3	—
200	9·76	19·06	44·60	81·10	138·6	250·6	258·11	479·6	651·6	786·4	—

contain about 149 species. Or in a population with $\alpha = 40$, 180 species would be produced by a sample of 1000 individuals.

Further, by following along one of the α curves it is possible to find the number of species in samples of different sizes from the same population. Thus if a sample of 1000 individuals for a population produced 73 species, then a sample of 10,000 from the same population should produce about 112 species, but a sample of 100 individuals would only contain about 34 species ($\alpha = 18$). In addition, on the diagram the standard error (as a percentage of the value of α) has been indicated by dotted contours. Thus a sample containing 100 individuals and 24 species gives $\alpha = 10 \pm$ about 17%, say $10 \pm 1{\cdot}7$; a sample of 1000 individuals and 46 species gives $\alpha = 10 \pm 0{\cdot}75$ (i.e. 7·5%); while a sample of 10,000 individuals containing 69 species gives $\alpha = 10 \pm 0{\cdot}45$ (4·5%). Thus the size of sample necessary to give α to any required degree of accuracy can rapidly be obtained from the figure.

Table 7 shows values of *S* correct to two decimal places for various combinations of α and *N*, and Table 8 shows the standard error of α to three significant figures for various values of *N* and α.

Table 8. *Standard error of α for different values of N and α*

α \ N	10	100	1000	10,000	100,000
1	0·504	0·288	0·141	0·091	—
5	2·785	0·860	0·430	0·282	0·209
10	6·46	1·60	0·719	0·445	0·321
20	15·82	3·19	1·52	0·712	0·495
50	49·87	8·79	2·67	1·359	0·891
100	153·7	20·42	5·04	2·27	1·41

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PART 3. A THEORETICAL DISTRIBUTION FOR THE APPARENT ABUNDANCE OF DIFFERENT SPECIES

By R. A. Fisher

(1) *The Poisson Series and the Negative Binomial distribution*

In biological sampling it has for some time been recognized that if successive, independent, equal samples be taken from homogeneous material, the number of individuals observed in different samples will vary in a definite manner. The distribution of the number observed depends only on one parameter, and may be conveniently expressed in terms of the number *expected*, m, in what is known as the *Poisson Series*, given by the formula

$$e^{-m}\frac{m^n}{n!}. \qquad (1)$$

Here n is the variate representing the number observed in any sample, m is the parameter, the number expected, which is the average value of n, and need not be a whole number. Obviously, m will be proportional to the size of the sample taken, and to the density of organisms in the material sampled. For example, n might stand for the number of bacterial colonies counted on a plate of culture medium, m for the average number in the volume of dilution added to each plate. The formula then gives the probability of obtaining n as the number observed.

The same frequency distribution would be obtained for the numbers of different organisms observed in one sample, if all were equally frequent in the material sampled.

If the material sampled were heterogeneous, or if unequal samples were taken, we should have a mixture of distributions corresponding to different values of m. The same is true of the numbers of different organisms observed in a single sample, if the different species are not equally abundant.

An important extension of the Poisson series is provided by the supposition that the values of m are distributed in a known and simple manner. Since m must be positive, the simplest supposition as to its distribution is that it has the Eulerian form (well known from the distribution of χ^2) such that the element of frequency or probability with which it falls in any infinitesimal range dm is

$$df=\frac{1}{(k-1)!}p^{-k}m^{k-1}e^{-m/p}\,dm. \qquad (2)$$

If we multiply this expression by the probability, set out above, of observing just n organisms, and integrate with respect to m over its whole range from 0 to ∞, we have

$$\int_0^\infty \frac{1}{(k-1)!}p^{-k}m^{k-1}e^{-m/p}e^{-m}\frac{m^n}{n!}\,dm,$$

which, on simplification, is found to have the value

$$\frac{(k+n-1)!}{(k-1)!\,n!}\,\frac{p^n}{(1+p)^{k+n}}, \qquad (3)$$

which is the probability of observing the number n when sampling from such a heterogeneous population. Since this distribution is related to the negative binomial expansion

$$\left(1-\frac{p}{1+p}\right)^{-k}=\sum_{n=0}^{\infty}\frac{(k+n-1)!}{(k-1)!\,n!}\left(\frac{p}{1+p}\right)^n,$$

it has become known as the *Negative Binomial distribution*. It is a natural extension of the Poisson series, applicable to a somewhat wider class of cases.

The parameter p of the negative binomial distribution is proportional to the size of the sample. The expectation, or mean value of n, is pk. The second parameter k measures in an inverse sense the variability of the different expectations of the component Poisson series. If k is very large these expectations are nearly equal, and the distribution tends to the Poisson form. If heterogeneity is very great k becomes small and approaches its limiting value, zero. This second parameter, k, is thus an intrinsic property of the population sampled.

(2) *The limiting form of the negative binomial, excluding zero observations*

In many of its applications the number n observed in any sample may have all integral values including zero. In its application, however, to the number of representatives of different species obtained in a collection, only frequencies of numbers greater than zero will be observable, since by itself the collection gives no indication of the number of species which are not found in it. Now, the abundance in nature of different species of the same group generally varies very greatly, so that, as I first found in studying Corbet's series of Malayan butterflies, the negative binomial, which often fits such data well, has a value of k so small as to be almost indeterminate in magnitude, or, in other words, indistinguishable from zero. That it is not really zero for collections of wild species follows from the fact that the total number of species, and therefore the total number not included in the collection, is really finite. The real situation, however, in which a large number of species are so rare that their chance of inclusion is small, is well represented by the limiting form taken by the negative binomial distribution, when k tends to zero.

The limiting value $k=0$ cannot occur in cases where the frequency at zero is observable, for the

distribution would then consist wholly of such cases. If, however, we put $k=0$ in expression (3), write x for $p/(p+1)$, so that x stands for a positive number less than unity, varying with the size of the sample, and replace the constant factor $(k-1)!$ in the denominator, by a new constant factor, α, in the numerator, we have an expression for the expected number of species with n individuals, where n now cannot be zero,

$$\frac{\alpha}{n}x^n. \qquad (4)$$

These two relationships enable the series to be fitted to any series of observational data, for if S is the number of species observed, and N the number of individuals, the two equations

$$S=-\alpha \log_e(1-x), \quad N=\alpha x/(1-x),$$

are sufficient to determine the values of α and x. The solution of the equations is, however, troublesome and indirect, so that to facilitate the solution in any particular case I have calculated a table (Table 9) from which, given the common logarithm

Table 9. *Table of $\log_{10} N/\alpha$ in terms of $\log_{10} N/S$, for solving the equation*

$$S=\alpha \log_e\left(1+\frac{N}{\alpha}\right), \text{ given } S \text{ and } N$$

$\log_{10} N/S$	0	1	2	3	4	5	6	7	8	9
0·4	0·61121	63084	65023	66939	68832	70701	72551	74382	76195	77990
0·5	0·79766	81526	83271	85002	86717	88417	90105	91779	93442	95092
0·6	0·96730	98356	99973	1·01579	03174	04759	06335	07902	09460	11010
0·7	1·12550	14220	15813	17331	18772	20136	21631	23120	24602	26077
0·8	1·27546	29008	30465	31916	33361	34801	36234	37663	39087	40506
0·9	1·41920	43329	44733	46133	47528	48919	50305	51688	53066	54440
1·0	1·55810	57177	58539	59898	61254	62605	63954	65299	66640	67979
1·1	1·69314	70646	71975	73301	74623	75943	77261	78575	79886	81195
1·2	1·82501	83805	85106	86404	87700	88994	90285	91574	92860	94144
1·3	1·95426	96706	97984	99259	2·00532	01804	03073	04340	05605	06869
1·4	2·08130	09389	10647	11902	13156	14409	15659	16908	18155	19400
1·5	2·20644	21886	23126	24365	25602	26838	28072	29305	30536	31766
1·6	2·32994	34221	35446	36670	37893	39114	40334	41553	42770	43986
1·7	2·45201	46414	47627	48838	50048	51256	52464	53670	54875	56079
1·8	2·57282	58484	59684	60884	62083	63280	64476	65672	66866	68059
1·9	2·69252	70443	71633	72822	74011	75198	76385	77570	78755	79939
2·0	2·81121	82303	83484	84664	85843	87022	88199	89376	90552	91727
2·1	2·92901	94075	95247	96419	97590	98760	99930	3·01099	02267	03434
2·2	3·04600	05766	06931	08095	09259	10422	11584	12745	13906	15066
2·3	3·16225	17384	18542	19699	20856	22012	23168	24323	25477	26630
2·4	3·27783	28936	30087	31238	32389	33539	34688	35837	36985	38133
2·5	3·39280	40426	41572	42717	43862	45006	46150	47293	48436	49578
2·6	3·50719	51860	53001	54141	55280	56419	57558	58696	59833	60970
2·7	3·62106	63242	64378	65513	66648	67782	68915	70048	71181	72313
2·8	3·73445	74577	75707	76838	77968	79097	80227	81355	82484	83611
2·9	3·84739	85866	86992	88119	89244	90370	91495	92619	93743	94867
3·0	3·95991	97114	98236	99358	4·00480	01602	02723	03843	04964	06084
3·1	4·07203	08322	09441	10560	11678	12795	13913	15030	16147	17263
3·2	4·18379	19494	20610	21725	22839	23954	25068	26181	27295	28408
3·3	4·29520	30632	31744	32856	33967	35079	36189	37300	38410	39520
3·4	4·40629	41738	42847	43956	45064	46172	47280	48387	49494	50601
3·5	4·51707	52814	53920	55025	56131	57236	58340	59445	60549	61653

The total number of species expected is consequently

$$\sum_{n=1}^{\infty}\frac{\alpha}{n}x^n=-\alpha \log_e(1-x),$$

so that our distribution is related to the algebraic expansion of the logarithm, as the negative binomial distribution is to the binomial expansion. Next, it is clear that the total number of individuals expected is

$$\sum_{n=1}^{\infty}\alpha x^n=\frac{\alpha x}{1-x}.$$

of N/S, we may obtain that of N/α. Five-figure logarithms are advisable, such as those in *Statistical Tables*. If x be eliminated from the two equations, it appears that

$$N=\alpha(e^{S/\alpha}-1), \quad S=\alpha \log_e\left(1+\frac{N}{\alpha}\right),$$

and

$$\frac{N}{S}=(e^{S/\alpha}-1)\div S/\alpha,$$

from which Table 9 has been constructed.

(3) *Fitting the series*

The use of the table is shown, using Williams's extensive data for the Macrolepidoptera at Harpenden (total catch for four years). Symbols + and − are used to indicate numbers to be added and subtracted respectively.

Symbol	Number	Common logarithm
S	240	−2·38021
N	15609	+4·19338
N/S	—	1·81317
From the table	log (N/S)	log (N/α)
	−1·81	−2·58484
	+1·82	+2·59684
Difference	0·01	0·01200
Proportional parts	0·00317	0·00380
	1·81317	2·58864

Then	Number	Common logarithm
N/α	—	−2·58864
N	—	+4·19338
α	40·248	1·60474

For constructing the distribution we should then calculate

$$x=\frac{N}{N+\alpha}=\frac{15609}{15649\cdot248}=0\cdot9974281.$$

The quantity α is independent of the size of sample, and is proportional to the number of species of the group considered, at any chosen level of abundance, relative to the means of capture employed. Values of α from different samples or obtained by different methods of capture may therefore be compared as a measure of richness in species. To this end we shall need to know the sampling errors by which an estimate of α may be affected.

(4) *Variation in parallel samples*

Whatever method of capture may be employed, it is to be expected that a given amount of activity devoted to it, e.g. a given number of hours exposure of a light-trap, or a given volume of sea water passed through a plankton filter, will yield on different occasions different numbers of individuals and of species, and, consequently, varying estimates of α. The amount of variation of these kinds attributable to chance must form the basis of all conclusions as to whether variations beyond chance have occurred in the circumstances in which two or more samples were made.

In strictly parallel samples, i.e. equivalent sampling processes applied to homogeneous material, the numbers caught of each individual species will be distributed in a Poisson series, and it easily follows that the same is true of the aggregate number, N, of all species. Since N is a large number of hundreds or thousands, this is equivalent to N being normally distributed with a variance equal to its mean, so that to any observed value N we may attach a standard error (of random sampling) equal to $\pm\sqrt{N}$.

For the variation of S we must obtain the distribution of species according to the number m expected in the sample; modifying expression (2) in the same way as (3) has been modified, this is found to be

$$\alpha e^{-\alpha m/N}dm/m. \qquad (5)$$

The probability of missing any species is e^{-m}, so that the contribution to the sampling variance of S due to any one species being sometimes observed and sometimes not, is

$$e^{-m}(1-e^{-m}).$$

Multiplying this by the frequencies in (5) and integrating over all values of m, we have

$$\alpha\int_0^\infty e^{-m(N+\alpha)/N}\left(1-\frac{m}{2}+\frac{m^2}{6}-\ldots\right)dm=\alpha\log_e\left(\frac{2N+\alpha}{N+\alpha}\right),$$

which is the sampling variance of S. For large samples this is approximately $(0\cdot6931)\,\alpha$.

Variations of S and N in parallel samples are not, however, independent. When present, a species must contribute on the average $m/(1-e^{-m})$ individuals, which exceeds the expectation in all samples by

$$\frac{me^{-m}}{1-e^{-m}},$$

and as the frequency of occurrence is $1-e^{-m}$, each species must contribute $m.e^{-m}$ to the covariance of S and N. The covariance is thus found to be

$$\frac{\alpha N}{N+\alpha}.$$

From these three values it is possible by standard methods to find the sampling variance of S in samples having a given number of specimens N, which is

$$V(S),\text{ given }N,=\alpha\log_e\frac{2N+\alpha}{N+\alpha}-\frac{\alpha^2N}{(N+\alpha)^2}$$

and, the variance of α,

$$V(\alpha)=\frac{\alpha^3\left\{(N+\alpha)^2\log_e\frac{2N+\alpha}{N+\alpha}-\alpha N\right\}}{(SN+S\alpha-N\alpha)^2}.$$

We may, therefore, complete the example of the last section by calculating the standard error of α. Using the values obtained, the variance comes to 1·1251, of which the square root is 1·0607.

The estimate obtained for α, 40·248, has, therefore, a standard error of 1·0607, available for comparison with like estimates.

(5) *Test of adequacy of the limiting distribution*

From the manner in which the distribution has been developed it appears that we never have theoretical grounds for supposing that k is actually zero;

but, on the contrary, must generally suppose that in reality it has a finite, though perhaps a very small, value. Our reasons for supposing this small value to be negligible must always be derived from the observations themselves. It is, therefore, essential to be able to test any body of data in respect to the possibility that in reality some value of k differing significantly from zero might fit the data better than the value zero actually assumed.

The most sensitive index or score by which any departure of the series of frequencies observed from those expected can be recognized, is found by the general principles of the Theory of Estimation, as, for example, in the author's *Statistical Methods for Research Workers*, to be

$$S\left\{a_n\left(1+\tfrac{1}{2}+\tfrac{1}{3}+\ldots+\frac{1}{n-1}\right)\right\},$$

when a_n is a number of species observed with n individuals in each. If the values of a_n conformed accurately with expectation, the total score would be equal to

$$\frac{S^2}{2\alpha}.$$

If, on the contrary, the series were better fitted by a negative binomial with a value of k differing from zero, we should expect the difference

$$S\left\{a_n\left(1+\tfrac{1}{2}+\tfrac{1}{3}+\ldots+\frac{1}{n-1}\right)\right\}-\frac{S^2}{2\alpha}$$

to show a positive discrepancy.

Applying this test to Williams's distribution for 240 species of Macrolepidoptera, one finds, after a somewhat tedious calculation,

$S\left\{a_n\left(1+\tfrac{1}{2}+\tfrac{1}{3}+\ldots+\frac{1}{n-1}\right)\right\}$	724·86
$\frac{S^2}{2\alpha}$	715·57
Difference	+9·29

The series, therefore, shows a deviation in the direction to be expected for the negative binomial, though apparently quite a small one. In order to test the significance of such discrepancies, I give in Table 10, for the same range of observable values of the average number of specimens in each species N/S, the values of i/S, where i is the quantity of information, in respect of the value of k, which the data supply.

Table 10. *The amount of information respecting k, supposed small, according to the numbers of individuals (N) and species (S) observed*

$\log_{10} N/S$	i/S	$\log_{10} N/S$	i/S
0·4	0·1971		
0·5	0·2882		
0·6	0·3914	2·1	3·1047
0·7	0·5054	2·2	3·3606
0·8	0·6295	2·3	3·6260
0·9	0·7639	2·4	3·9009
1·0	0·9076	2·5	4·1854
1·1	1·0608	2·6	4·4791
1·2	1·2232	2·7	4·7825
1·3	1·3950	2·8	5·0954
1·4	1·5762	2·9	5·4178
1·5	1·7665	3·0	5·7498
1·6	1·9661	3·1	6·0912
1·7	2·1751	3·2	6·4421
1·8	2·3934	3·3	6·8026
1·9	2·6211	3·4	7·1726
2·0	2·8582	3·5	7·5521

Entering the table with our value 1·81317 for $\log_{10} N/S$ we have $i/S = 2{\cdot}4656$, or $i = 591{\cdot}7$. This quantity may now be used for two purposes. In the first place it is the sampling variance of the discrepancy observed, so that, taking its square root, the standard error is found to be 24·33. This suffices to test the significance of the discrepancy, since $9{\cdot}29 \pm 24{\cdot}33$ is clearly insignificant.

If, on the contrary, a significant discrepancy had been found, an estimate of the value of k required to give a good fit to the data could be made by dividing the discrepancy by i. In fact

$$\frac{9{\cdot}29}{591{\cdot}7} = 0{\cdot}016$$

would have been the value of k indicated by the data, if any value other than zero had been required.

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SUMMARY

Part 1. It is shown that in a large collection of Lepidoptera captured in Malaya the frequency of the number of species represented by different numbers of individuals fitted somewhat closely to a hyperbola type of curve, so long as only the rarer species were considered. The data for the commoner species was not so strictly 'randomized', but the whole series could be closely fitted by a series of the logarithmic type as described by Fisher in Part 3. Other data for random collections of insects in the field were also shown to fit fairly well to this series.

Part 2. Extensive data on the capture of about 1500 Macrolepidoptera of about 240 species in a light-trap at Harpenden is analysed in relation to Fisher's mathematical theory and is shown to fit extremely closely to the calculations.

The calculations are applied first to the frequency of occurrence of species represented by different numbers of individuals—and secondly to the number of species in samples of different sizes from the same population.

The parameter 'α', which it is suggested should be called the 'index of diversity', is shown to have a regular seasonal change in the case of the Macrolepidoptera in the trap. In addition, samples from two traps which overlooked somewhat different vegetation are shown to have 'α' values which are significantly different.

It is shown that, provided the samples are not small, 'α' is the increase in the number of species obtained by increasing the size of a sample by e (2·718). A diagram is given (Fig. 8) from which any one of the values, total number of species, total number of individuals and index of diversity (α), can be obtained approximately if the other two are known. The standard error of α is also indicated on the same diagram.

Part 3. A theoretical distribution is developed which appears to be suitable for the frequencies with which different species occur in a random collection, in the common case in which many species are so rare that their chance of inclusion is small.

The relationships of the new distribution with the negative binomial and the Poisson series are established.

Numerical processes are exhibited for fitting the series to observations containing given numbers of species and individuals, and for estimating the parameter α representing the richness in species of the material sampled; secondly, for calculating the standard error of α, and thirdly, for testing whether the series exhibits a significant deviation from the limiting form used.

Special tables are presented for facilitating these calculations.

REVIEWS

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This number contains five original papers, two reviews and a part of the Biological Flora. The number is mainly devoted to algal ecology. In the first paper, J. W. G. Lund deals with the algae of certain ponds in Richmond Great Park, with particular reference to those of the bottom deposits. Striking changes of the algal communities are shown to be correlated with stability of the substratum, with *p*H value and with seasonal changes related to the changes in organic matter, the conclusions being supported by the results of laboratory cultures. S. P. Chu describes new methods of successfully growing planktonic algae in laboratory cultures, these being based on the use of dilute solutions resembling natural surface waters in composition. Winifred Pennington has investigated the changes in nitrogen taking place in nitrogen-rich cultures of mixed algae. Both ammonia and nitrate were absorbed, and nitrite produced from each of these substances. Considerable losses of total nitrogen were demonstrated, though these may have been due to bacteria. From collections covering nearly four years, A. Malins Smith describes the algae of a small acid bog, supplied with nitrate rich drainage water. The algae, mostly green, fall mainly into two groups, those of free water and those of *Sphagnum*. The relations between algae abundance and such factors as temperature, humidity and the chemical properties of the waters are critically discussed. E. M. O. Laurie gives a detailed study of the variation of dissolved oxygen in a small Welsh upland pond and its inflowing stream. The seasonal and diurnal cycles are analysed in detail and the variations shown to depend on temperature, plant photosynthesis and respiration and oxygen consumption by organic matter.

An additional part of the Biological Flora is included dealing with *Aster tripolium* compiled from data provided by V. J. Chapman, by A. R. Clapham, W. H. Pearsall and P. W. Richards. There are reviews on the *Journal of Animal Ecology* and on ecological crop geography.

W. H. PEARSALL

SEA-FISH POPULATIONS

E. S. Russell (1942). *The overfishing problem. De Lamar Lectures delivered in the School of Hygiene of the Johns Hopkins University, Baltimore.* 130 pp., 16 figs. Cambridge University Press. Price 7*s.* 6*d.*

The history of the deep-sea fisheries since the introduction of steam has been essentially the same for many species. Through the discovery of new grounds and new techniques there is an increase in total catch to a point where, despite greater efforts, the catch begins to fall and to consist less and less of good-sized fish. But before the evidence from total landings becomes clear, statisticians can show that the catch per unit of effort (length of gear employed, number of hours of fishing) has been falling for some years. Proofs of this decline are not always easily obtained, for there are variations in brood strength, difficulties in sampling, huge environmental changes and a severe lack of control populations in which the extent of natural mortality can be determined. Evidence about natural mortality is that it is low among haddock before they are of nettable size; that among the few virgin fisheries studied there was much better survival; and that marking experiments prove there is a high mortality due to fishing alone: up to 73 % per annum among North Sea plaice.

If, therefore, natural mortality is small in relation to the catch (as it almost certainly is), and if there are plenty of young fish (which there usually are even in an overfished stock), then a simple formula proves that the condition for maintaining the highest annual catch depends almost entirely upon growth rate being at its greatest—hence that fisheries should be regulated to secure this. As growth is fastest when least energy is required for maintenance, commercial fishing may improve this rate by reducing competition for food among overcrowded fry and by removing old and slow-growing fish. On the other hand, fishing is very wasteful of the fast-growing fish just below marketable size which it kills and rejects.

Theoretically a stock of fish can be stabilized so that by very intense fishing (as usually practised) large numbers of small fish are obtained, whereas by less vigorous operations the fish have a chance to grow bigger and equal or exceed in weight what they lack in numbers. The optimum level is obviously where the greatest weight of fish is caught for the least effort: an optimum which cannot be precisely stated from existing data. That theory is borne out in practice has been shown since 1932 in the Pacific halibut fishery where, because of restrictive regulations, the same weight of fish was being caught in five months as used previously to be taken in nine.

This short and very readable book is primarily about an industry, and, as the author makes clear, is based upon a vast body of scientific data to which he mostly cannot refer in detail. Consider the following: 'The stocks of fish in the North Sea are more or less self-contained', or 'The cod stocks...have greatly increased...owing to large-scale...warming up of these waters'. Simple statements like these cover a vast accumulation of data by workers in many countries, not least among them Dr Russell and his co-workers in the Fishery Investigations of the Ministry of Agriculture and Fisheries. Yet compared with the enormous benefits which the industry would derive from scientific control, it is equally obvious that the indispensable value of the basic scientific investigations is nothing like fully realized. This book is particularly revealing of the way an apparent miscellany of such papers fits into the vast mosaic of fishery work.

It is fortunate that these lectures were prepared at the time they were, for by the end of the present war the stock of fish will have reached a high level; and through post-war planning and international co-operation this level could be maintained. Such action would help to solve the looming difficulty of how to have cheap food and yet pay good wages to the primary producer. Few animal population problems in this country have advanced to the stage where political action can be backed by so impressive an accumulation of facts. Other biologists should anxiously examine the official post-war attitude towards control of deep-sea fishing for signs of whether administrators really do intend to accept scientific advice.

DENNIS CHITTY

ECOLOGY IN INDIA

Indian Ecological Society (Founded 1941). First Annual Report. (Published 1942. Hon. Secretary and Treasurer: Dr F. R. Bharucha, Botany Dept., Royal Institute of Science, Bombay 1.)

This new Society was founded during the Indian Science Congress at Benares in January 1941, the idea being to have some organization working with ecological ideas and methods, which could help to co-ordinate the results of various activities in forestry, soil survey, natural history, conservation, and their underlying sciences, and so begin to build up a preliminary picture of Indian plant and animal communities and the environments they live in. The intention is to have meetings and excursions, and to publish bulletins abstracting Indian work on the whole subject, and to try and organize definite ecological surveys. Among other items mentioned is the intention 'to give addresses of firms making reliable apparatus for ecological work', an idea which might well be developed also in this country, with advantage to field workers. At present, the only primary research work issued by the Society is in the form of reprints of papers published elsewhere. These investigations include studies of various plant communities (mangroves, marsh plants, etc.), soils, and two papers on birds. It is to be hoped that the new Society, although not yet in a financial position to undertake a journal of its own, will act as a useful focus for personal contact and discussion among Indian ecologists. Its progress will be watched with very friendly interest by members of its counterpart in this country.

CHARLES ELTON

THE PAGEANTRY OF BREEDING

E. A. Armstrong (1942). *Bird display.* 382 pp. and 40 photos. Cambridge University Press. Price 21*s.*

The ecologist's interest in behaviour is primarily from an adaptational point of view. This book is concerned mainly with intraspecific elaborations, all tending to secure the successful meeting of the sexes and reproduction with as little disturbance as possible. Competition within the species impinges upon ecological ideas chiefly because of the limitations of density (e.g. via territory) which are imposed. From this point of view there is much in this book that will interest the ecologist indirectly. Emphasis is placed upon the nice balance which is maintained between conspicuousness for finding and stimulating mates and the dangers which may come from carrying such conspicuousness to excess. In this connexion the contention of the author (perhaps not quite sufficiently substantiated as yet by facts) that in species, which hold leks or courts, the sex ratio is biased heavily in favour of females and polygyny is the rule, thus lessening the danger of scattered conspicuous males being preyed upon and their mates being delayed in breeding, has considerable force. True, the author thinks that a biased sex ratio has been the cause of polygynous habits, whereas it is just as likely—perhaps more so—that the unequal sex ratio is the effect.

From a psychological point of view, surprise, both in colour and attitude, is stressed as important in stimulating a mate to successful copulation. This is often attained by hidden colours, which are flashed into view (e.g. the buccal cavity of gulls, auks, etc.). A further view of such an arrangement of more interest to the ecologist would be the avoidance of carrying about conspicuous colours, which would attract the attention of predators.

Generally speaking the book follows a logical sequence and carries the reader from point to point with painstaking documentation. Thus from nest-building one is taken on to ceremonial gaping and then disablement reactions. Greeting ceremonies lead on to display behaviour, social ceremonies, communal displays; finally, the significance of display generally is discussed, the treatment not being limited to British birds.

With such extensive documentation it is queer that statements of fact are often interspersed without any authority. Thus on p. 270 four statements are made in five lines about the method of recognizing a mate in different species, none of which is substantiated. Presumably the references have been given before (and it would certainly mean an extension of what has already been a very great labour to repeat them), but one is not sure; and occasionally the impression is given that the observations are the author's own (which may of course be the case).

Altogether this is a very useful book because it draws together so much scattered literature and gives cohesion to a very diffuse subject.

H. N. SOUTHERN

THE BED-BUG'S WORLD

(*a*) **Medical Research Council (1942).** *Report of the Committee on bed-bug infestation.* M.R.C. Special Report Series, No. 245: 64 pp. and 9 text-figures. H.M. Stationery Office, London. Price 1*s.*

(*b*) **C. G. Johnson (1942).** *The ecology of the bed-bug,* Cimex lectularius *L., in Britain: Report on research, 1935–40.* Journal of Hygiene, Cambridge, Vol. 41: 345–461. 39 text-figures.

The first of these publications contains sections on 'The ecology of the bed-bug', by P. A. Buxton and C. G. Johnson; 'Chemical properties of insecticides, in relation to the control of bed-bugs', by J. W. Munro and A. B. P. Page; 'The development of methods for disinfesting houses and furniture', by S. A. Ashmore and A. W. McKenny-Hughes; 'Domestic hygiene in the prevention and control of bed-bug infestation', by W. C. Gunn; 'Investigation of the toxicity to man of insecticides used against the bed-bug', and 'Building design in relation to bed-bug infestation (with a note on air-raid shelters)' from the Building Research Station. The present review will deal almost entirely with the first section, on ecology of populations, and with Johnson's separate paper, which contains much of the basic observation and experiment on this aspect. The root problem of fumigation has always been to dispense with hydrogen cyanide, which is very effective but also dangerous. Sulphur fumes are ineffective in killing eggs of bed-bugs, and also damage household goods. Orthodichlorobenzene had a good start, but it was then found to be toxic, at any rate to laboratory animals, even at very low concentrations. The most promising work has been with heavy naptha as a vapour, since it is effective and relatively safe. Gunn's approach has been from the human end, with intense house-cleaning, advice and follow-up inspections. All this important control experimentation was concerned, however, with a living population, whose distribution and potentialities were still very vaguely understood when these investigations began less than ten years ago.

The summary by Buxton and Johnson is certainly needed, to bring into focus the main conclusions of

Johnson's extremely complex and involved research on the bugs themselves. In the clarity and interest of this shorter summary we can discern the master hand that wrote *Animal life in deserts* and has fought a consistent battle against obscurity and dullness in ecological writing. It is rather interesting to compare statements made in the present summary, with a remark in Buxton and Hopkins's monograph, *Researches in Polynesia and Melanesia*, published in 1927, where the ecology of mosquitoes carrying elephantiasis is the central theme. 'In this report much attention is given to the ecology of the insects, that is to say, their relation to the climate, flora and fauna. Ecology is a difficult study, because its range is so wide, but to me it appears to be important, as it opens up the possibility of attaining natural control.' I can remember six years before that, being asked by a senior zoologist while lying in a tent on a cold Arctic summer night, 'Tell me, what *is* ecology?'; while a still more senior zoologist in the same year said to me: 'Ecologists? Are they not an obscure sect of the followers of Lamarck?' It was only two years before that I had heard of the subject myself, through the classical book of Shelford. Now, Buxton and Johnson write: 'The centre of the problem nowadays, and the point of greatest interest to the health officer, whether he knows it or not, is the question of *insect population*; to him the important question is whether the bed-bug (or other pest) is abundant enough to cause harm or annoyance, or to transmit disease. It therefore seems certain that future work on the bed-bug, and on many other sides of applied biology, will become more and more quantitative, demographic, and mathematical, because the object of study is the normal, wild bed-bug population.' Ecology on the march!

How recent the ecological approach has been is illustrated by our knowledge of temperature conditions as they affect bed-bug physiology and reproduction. Johnson notes that all work previous to 1935 had been done with laboratory populations kept at temperatures of 72–104° F., whereas the room temperatures which are critical in the field problem in this country are nearly all lower ones, and further study had therefore to be made on the range 32–72° F. This study has produced a large number of valuable 'biological constants', e.g. the egg takes ten times as long to hatch out at 55·4° F. as it does at 95° F. There was also much leeway to be made up in the actual measurement of room temperatures in various kinds of houses: practically nothing was known in 1935 about the temperatures in which most English people live when they are indoors. This knowledge has turned out to be absolutely vital in bed-bug control, because if a bedroom is largely unheated, any bed-bugs living in it during the winter will be severely checked in population growth, by the effects on both reproduction and mortality. That is to say, even with adequate food supply, a bed-bug population in our climate cannot flourish without artificial heating in the winter months. It is pointed out that a bed-sitting room (occupied through the day, and at any rate heated in winter evenings) will be a better environment for bugs than the unheated bedroom of the ordinary better-class English house; but that central heating (let our American friends and visitors note!) will again provide comfortable bedrooms for bed-bugs.

Research was done on all stages of the bug, and the effects of feeding and microclimatic conditions on egg hatching, on the five nymphal stages and on the adult. The interconnexion between the different factors makes a simple statement about the optimum conditions hard to give. For instance, each nymph must have a blood-meal before it can moult; but if it is kept in the cold, its ability to moult, even after a meal and higher temperatures, is impaired. And this phenomenon is most marked in the early instars. The experiments on mortality give some idea of the expectancy of life in populations kept at different temperatures in the laboratory. The maximum length of life of a mated female was highest at 55·4° F. (565 days), the mean length of life being 360. The lowest longevity was at 73·4° F. (of the temperatures studied), with 127 maximum and 69 days mean length in days. These were fasting bugs!

The ordinary *Cimex lectularius* of man was fed experimentally on different human beings, on mice and on domestic fowls, and there were differences in growth and reproduction according to which host had been used. Indeed, the mice, being hotter, were more attractive, so that the bugs sucked more blood from them, grew faster and survived better, than on man or fowl. But fasting bugs could live longer if they had been drinking human blood. And, with freely associated populations in cages, the mice ate quite a large number of the bugs, which would have cancelled out the attractions of mouse blood.

A question of profound interest to us is what makes bed-bugs become active and successfully seek their human host. Johnson discusses this problem, though admitting that knowledge is still in an early stage, and one-factor experiments on behaviour limited or lacking. Observations by Mellanby have certainly shown the existence of a 24 hr. rhythm in activity with a peak just before dawn, and Johnson made notes on the wanderings of bed-bugs. It is likely that the bugs are able to perceive the heat of the air through their antennae, and are also affected by humidity, light, and their physiological state at any moment. At any rate they seem to get there, and further ecological research should tell us how they do it!

After reading the complex interaction of different variables, internal and external, which Johnson describes, one is ready to agree with his conclusion that 'the whole subject must now be approached from a different angle and the deductive method from laboratory data must be supplemented, and perhaps temporarily replaced, by an inductive one which has as its basis quantitative work in the field and in experimental rooms'. It seems likely that the limiting factors that are critical for practical control will more quickly be discovered in this way. But the investigation so far done provides a model for applied entomology of the kind, and contains figures of the greatest interest to population ecologists and insect physiologists. The Committee has done a first-class job in the time allotted to it. CHARLES ELTON

THE GROWTH OF ORNITHOLOGY

James Fisher (1942). *The birds of Britain.* 48 pp., 12 coloured plates and 26 other illustrations. (In the series: *Britain in Pictures.*) William Collins, Sons and Co. Ltd., 48 Pall Mall, London, S.W. 1. Price 4*s.* 6*d.*

In his book on North Rona, Fraser Darling remarked that 'the aim of science should certainly be to remove the mystery from natural phenomena, but not to take away wonder or that quality of nature which allows for the development and play of aesthetic appreciation', and I suggested in a review of it that most ecologists had lost this power of wonder in their effort to tear away the

mystery. We have insisted on such precise and specialized description and analysis that we have, as ecologists, been prone to brush aside as irrelevant and dangerous to our judgement the other attributes of the natural scene, 'whether', as the Apocrypha says, 'there was a whistling wind, or a melodious noise of birds among the spreading branches, or a measured fall of water running violently, or a harsh crashing of rocks hurled about, or the swift course of animals bounding along unseen....' At any rate, whatever sense of the miraculous, the beautiful or the majestic animal ecologists may have felt during the course of their work in the field, they have ably concealed in most of their publications. The thirsty reader of 'precision literature' in ecology stumbles thankfully into an occasional oasis of Leopold or Murphy or Buxton, but on the whole has to rely for aesthetic stimulus on his own memories of field experiences.

At times one longs even for the rotund style of Von Humboldt, the first great ecological traveller: 'From the rich luxuriance of organic life the astonished traveller suddenly finds himself on the dreary margin of a treeless waste.' The modern ecologist does not write: 'Like a limitless expanse of waters, the Steppe fills the mind with a sense of the infinite, and the soul, freed from the sensuous impressions of space, expands with spiritual emotions of a higher order.' And yet Humboldt goes on to describe the rocks and vegetation and animals and people of the steppes and deserts, just as scientifically and a great deal more eloquently than we ever do in scientific journals.

We must therefore be grateful to anyone who is able, especially within the restrictions of war-time printing, to convey successfully both the scientific and aesthetic aspects of a group of animals as effectively as Mr Fisher has done in this book. The illustrations, selected from books of various periods, transport one at once into the brilliant and mysterious reality of animal community life. Audubon's perilous dive-bombing arctic tern recalls to me the shallow inshore waters of a Spitsbergen fjord, with *Gammarus locusta* taking cover among the stones and seaweed; Joseph Wolf's long-eared owl suggests a morning crawling among the interlacing branches of a young larch plantation in the Highlands in search of middens of owl pellets, and the finding of an owl that had died from starvation after the crash of a vole population; Edward Neale's partridge with young (the 'Hungarian partridge' of Canadian and American introducers) makes one think of the plumpness and lustre of the paired birds sitting conspicuously about in our fields in spring, as if designed by heaven for a census from the roads. The rest of the illustrations give similar pleasure and stimulus, and even the few stiff ones that are included to show the earlier museum style are interesting for comparison.

The text is fully up to the promise of the illustrations, being intelligent, clear and packed with neatly docketed facts that have probably never been brought all together before, although some of them were lying about in works like the *Handbook of British Birds*, the *Encyclopaedia Britannica* and *Whitaker's Almanack*. So, we are given the areas of different kinds of major habitats; the number of birds in the country; the number of species, divided into migrant and resident and so on; the number of species in any major habitat (here given as about thirty); the species peculiar to Britain; the importance of hedges; the Holocene history of bird communities; the curious differences in northern range between the British and Continental populations of some birds like the nightingale and the nuthatch; the effects of deforestation and afforestation, of collectors, of preservation measures, of shooting; the decrease of raptorial birds; migration; the history of ornithologists; modern bird watching; ending with the dream of an El Dorado in which everything is known and everything is put on to electrically operated punch-cards!

There is an appendix with lists of the English (but not the Latin) names of British birds, divided into various classes of movement and abundance. The text examples to illustrate various matters are well chosen and occasionally elaborated upon. Throughout, there is a fresh outlook and a firm appreciation of our fauna as unstable, changing, dynamic, and of these changes being due not only to human influences but also (as with the fulmar) to quite unknown natural causes. The reader should note, however, that most ecologists would refuse to accept the author's estimates of the total populations of British birds—estimates based on a number of extrapolations that still remain to be substantiated by many more field surveys. To say on the first page of an otherwise sound book that 'Every spring about a hundred and twenty million land birds take up territories, build nests and raise their young upon these fifty-seven million acres' is entirely to mislead the public as to the degree of precision our present census sampling methods have reached. In any case, the figure, whatever it is, would be falling through natural mortality, at a definite, though unknown, rate during the three breeding phases mentioned.

It would be a good thing if the author could develop in monograph as well as in this brief summary, some of the interesting subjects that are touched upon, and which have not yet been given much attention by ecologists: the history of game preserving, the decrease in raptorial birds, the number of birds in an animal community. As to the style of the book, it is exceptionally easy to read. There is here and there a certain pompousness (the guillemot's 'clumsy-looking flight is purposeful'—but can you blame the guillemot?; 'there is nothing tropical about England'—we know that by bitter experience, and so now do a great many Americans); sometimes a slight hang-over from the you-and-me atmosphere of broadcasting ('I am afraid I am rather pessimistic about the kite's future'); an occasional Puss-in-Boots attitude towards the British bird population—an overstepping of the line between interpretation and showmanship. With such personal enthusiasm for a single group one should be tolerant, even when the group in question contains less than 1% of the British fauna. (It is inevitable that comparatively large flying animals should have less need for cover than other classes and should form a more conspicuous element in the landscape; with this has gone the astonishing evolution of striking colour patterns that makes birds so popular an object of field study.) With the publisher's fatuous blurb on the cover one can only be impatient. But one can express gratitude for a first-class piece of ecological journalism that is free from nearly all the faults of its class, and for the exciting quality of the illustrations. With a less talented compiler the comments I have made above would be hardly worth their weight. But we have here an example of liaison writing, the kind of bridge that is going to be needed more and more, if wild life is to receive intelligent and sympathetic treatment from the forty-five million people that jostle it on a small archipelago. Therefore ecologists must encourage and welcome all such liaison work, yet remain jealous to see that it reaches a high standard of integrity and that publishers co-operate in a proper effacement and modesty of the persons who undertake the onerous job of interpreting the research of others.

CHARLES ELTON

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the paper to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W.1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, B. M. Hobby, Barrington Moore, F. T. K. Pentelow, H. N. Southern and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Stephenson, T. A. (1942). 'Causes of intertidal zonation.' Nature, Lond. 150: 158.

Summary of the remarks of several speakers on plants and animals. The complex of factors is considerable; but in South Africa sea temperature appears to be the dominant agent in determining distribution around the coast. Zonation on open rock depends largely on the amount of exposure to desiccation, heat, light and wave action.

Spurway, H. (1943). 'Newt larvae in brackish water.' Nature, Lond. 151: 109–10.

Larvae of *Molge palmata* in a fresh-water pool near the shore of Carradale Bay, Argyll, continued to live and metamorphose successfully in this pool or water taken from it, when the salinity had been increased by tidal invasion up to 5·6% of sea water, and subsequently diluted after a day or so by rain water. A newt placed in 68·3% sea water died in 1 hr. 40 min. A species of *Gammarus* resembling *G. duebeni* lived in the same pool. It is concluded that the newts could live and develop successfully in pools subject to temporary brackish water conditions.

Went, A. E. J. (1941). 'Salmon of the Owenduff (Ballycroy) River.' Proc. R. Irish Acad. B, 47: 161–78.

Salmon grow much less rapidly than trout in fresh water, much faster in the sea.

Went, A. E. J. (1942). 'Salmon of the River Erne. Results of the examination of a small collection of scales and data.' Sci. Proc. R. Dublin Soc. 22: 471–80.

As in the River Shannon, two types of smolt were found, one of which did and the other did not make growth in the spring prior to migration.

Orton, J. H. (1942). 'Biology of young salmon (*S. salar*, Linn.).' Nature, Lond. 150: 21–2.

A diagram is given broadly summarizing data for the Welsh Dee. Overall growth even during good feeding is limited by low spring temperatures and later (in the male) by development of the gonads and spawning.

Burke, F. (1942). 'Insect fauna of a brine-pit.' Nature, Lond. 150: 610–11.

A deep pit on the border of Cheshire and Flintshire had a surface water 25 ft. across, salinities at or near the surface of 7·9–9·5 NaCl per mille, and *p*H 6·5–8·7, varying little throughout the year. The chief insect inhabitant, very abundant, was the Ephydrid fly, *Ephydra riparia*, highly parasitized by an unnamed Pteromalid. The Stratiomyiid fly, *Nemotelus notatus*, was fairly numerous, and another fly, *Atissa pygmaea*, was present in lesser numbers than the others. These three species were breeding in the brine pool. Several other insects were observed as visitors to it: *Corixa* sp., the beetles *Ilybius fulginosus*, and *Hydroporus* sp. There is a photograph of the pool and its surroundings, and of the hind parts of *Ephydra riparia*.

Wollaston, G. H. B. (1942). '*Aëpophilus bonnairei* Sign. (Hem., Aëpophilidae) in North Devon.' Ent. Mon. Mag. 78: 204.

This bug was found in rock crevices of the intertidal zone in the company of water mites which were thought to play some part in its general life.

Gross, F. & Raymont, J. E. G. (1942). 'The specific gravity of *Calanus finmarchicus*.' Proc. Roy. Soc. Edinb. 61: 288–96.

The eggs are not buoyant but sink about 36 m. in the 24 hr. taken to hatch out. Stage V, *Calanus*, which is the most important form in which the species overwinters, has the lowest density of any stage. It is possible that this buoyancy enables the animal to maintain itself at suitable depths with the minimum waste of energy.

Poole, H. H. (1942). 'Illumination and visual range under water.' Nature, Lond. 150: 337–9.

Some attempts at measuring light penetration have failed to take account of the insensitivity of the photometer to light scattered at wide angles from the vertical. Visibility of an object depends on the contrast between it and the field around it and thus cannot be related directly to intensity of light penetration.

(*b*) Fresh water

Laurie, E. M. O. (1942). 'The fauna of an upland pond and its inflowing stream at Ystumtuen, North Cardiganshire, Wales.' J. Anim. Ecol. 11: 165–81.

The pond is at approximately 1000 ft., the water is slightly acid, low in calcium, and well oxygenated throughout the year. Animals in the stream were stone-clinging, those in the pond were vegetation and mud dwelling. At least 98 species were collected in the four plant-associations and two other habitats in the pond.

Laurie, E. M. O. (1942). 'The dissolved oxygen of an upland pond and its inflowing stream, at Ystumtuen, North Cardiganshire, Wales.' J. Ecol. 30: 357–82.

Diurnal changes in oxygen content of the stream were mainly correlated with temperature changes, those in the pond with the combined result of temperature and animal and plant activities. Seasonal changes were not dominated by the decomposition of organic matter, but by atmospheric oxygen. The detailed interaction of these factors is discussed on the basis of weekly determinations of oxygen and temperature for over a year.

Whitney, R. J. (1942). 'Diurnal fluctuations of oxygen and *p*H in two small ponds and a stream.' J. Exp. Biol. 19: 92–9.

The oxygen content of the ponds built up during the day decreased at night when photosynthesis stopped. When comparing oxygen conditions in different habitats, comparisons made at one hour of the day may be quite different from those at another. A diurnal series should therefore be taken in each.

Mortimer, C. H. & Worthington, E. B. (1942). 'Morphometric data for Windermere.' J. Anim. Ecol. 11: 245–7.

Results of a detailed bathymetric survey are recorded in a table showing the area enclosed by each 5 m. contour and the volume of water in each layer between contours. Computed volumes are estimated to be within 5% of true values.

Jenkin, P. M. (1942). 'Seasonal changes in the temperature of Windermere (English Lake District).' J. Anim. Ecol. 11: 248–69.

Monthly temperatures for a year, November 1931 to October 1932, taken by water bottle at seven or eight depths are practically the same at all depths in winter and show stratification in the upper layers in summer. The figures are used for working out the circulation throughout each season, and computing the heat storage. Water density at different levels is shown graphically in a comparison between lakes of 'Coastal' and 'Continental' type.

Went, A. E. J. & Frost, W. E. (1942). 'River Liffey survey. V. Growth of brown trout (*Salmo trutta* L.) in alkaline and acid waters.' Proc. R. Irish Acad. B, 48: 67–84.

Trout from alkaline waters of mean *p*H 7·9 grow quite big; those from higher up river, mean *p*H 5·6, seldom exceed 4 oz. The larger size is attained because there is a longer period of rapid growth and faster growth during the (winter) period of slow growth.

Gardiner, A. C. (1942). 'More about trout growth: some observations and suggestions.' Salm. Trout Mag. Lond. No. 106: 231–45.

A review of the theories so far adduced to explain the very variable growth rate of brown trout in different waters, with particular reference to the hypothesis that it is related to the calcium content of the water.

Frost, W. E. (1942). 'R. Liffey survey IV. The fauna of the submerged "mosses" in an acid and an alkaline water.' Proc. R. Irish Acad. B, 47: 293–369.

There were more species among the bryophytes at the alkaline station; but total number of organisms, the proportion of each and their seasonal fluctuations were remarkably similar.

Browne, J. Balfour- (1942). 'The aquatic Coleoptera (including Hydrophilidae, Sphaeridiinae) of North Wales.' Ent. Mon. Mag. 78: 273–80.

Records from Anglesey (61 species), Carnarvon (123), Denbigh (68), Flint (48), Merioneth (55), and Montgomery (15).

Daniels, E. T. (1942). 'Rediscovery of *Aphelocheirus montandoni* Horvath in Norfolk.' Entomologist, 75: 165–6.

This water-bug has not been seen in Norfolk since 1874.

Hynes, H. B. N. (1942). 'A study of the feeding of adult stoneflies (Plecoptera).' Proc. R. Ent. Soc. Lond. A, 17: 81–2.

Experiments which indicate that access to food is necessary for the survival of adult *Nemoura variegata*.

Hickin, N. E. (1942). 'Larvae of the British Trichoptera 5 [–7].' Proc. R. Ent. Soc. Lond. A, 17: 119–22 [123–6, 134–7].

Describes larva and habitat of *Odontocerum albicorne*, *Silo pallipes* and *Phryganea grandis*.

Taylor, C. B. (1942). 'The ecology and significance of the different types of coliform bacteria found in water. A review of the literature.' J. Hyg., Camb. 42: 23–44.

It has often been considered that presence of *Bacterium aerogenes* indicated pollution from soil or plants and not from animals or man. Insufficient evidence was found to support this view.

Taylor, C. B. (1941). 'The distribution of bacteria in lakes and their inflows.' Abstr. Proc. Soc. Agric. Bact.: 10–12.

During winter, plate counts of bacteria were much the same from all depths, though variable from week to week. In summer bacteria were less numerous below the thermocline.

Taylor, C. B. (1941). 'The types of coliform bacteria in rivers and lakes.' Abstr. Proc. Soc. Agric. Bact.: 13–15.

Purity of drinking water cannot be determined from the proportion of so-called faecal to non-faecal types, i.e. *Bacterium coli* to *B. aerogenes-B. cloacae* types. The former was found to be relatively more abundant in pure than in polluted water.

(*c*) Land

Marshall, F. H. A. (1942). 'Exteroceptive factors in sexual periodicity.' Biol. Rev. 17: 68–90.

Summarizes the large body of recent work on this subject in the vertebrates. Gonadal cycles are in most cases adjusted to the seasonal cycle by stimuli arising from light and ultra-violet irradiation. The cycles may be considerably modified by stimuli arising from the relationships between the two sexes or between the female and her offspring, and the sexual processes of the two sexes are often synchronized by display and courtship phenomena.

Manley, G. (1942). 'Meteorological observations on Dun Fell, a mountain station in Northern England.' Quart. J. R. Met. Soc. 68: 151–65.

Observations were kept for three years at 2735 ft. in the Northern Pennines well above the tree line. These are compared with those from summit stations elsewhere. This is the first series of 'mountain' observations available in England.

Lewis, L. F. (1942). 'Secular trend of temperature at Oxford.' Quart. J. R. Met. Soc. 68: 61–2.

There was a rapid increase in the 20-year average in winter (December–February) from the 20 years ending 1898 to the 20 years ending 1928. Subsequently there was a fall which probably denotes the beginning of a real downward trend. The summer curve showed a minimum from 1920 onwards until towards the end of the period when there was a fairly sharp rise. A curve representing the difference between summer and winter averages is given.

Glasspoole, J. & Hogg, W. H. (1942). 'Serial monthly values of mean temperature over the British Isles, 1881–1940, and annual values 1866–1940.' Quart. J. R. Met. Soc. 68: 45–57.

Also gives serial monthly and annual values for England and Wales, Scotland and Ireland separately, 1901–40. The values for the British Isles are discussed and a frequency table is given for values within specified limits for each month.

Williamson, K. (1942). 'Field notes on breeding pairs of willow-warbler and chiffchaff.' Northw. Nat. 17: 26–35 and 173–8.

Observations made in County Antrim. *Willow warbler.*—Length of feeding periods of female given both when incubating and brooding, until the tenth day. Courtship display and injury feigning described. Chart gives periods of brooding relative to times of male song and female call notes. *Chiffchaff.*—Describes five nests and gives details of building activity in the case of one. The eggs were laid at day intervals between late evening and early morning and in the one case where data were available the incubation period was 14 days. Song charts are given.

N——, J. B. (1942). 'Bird song at dawn.' Vasculum, 27: 22.

Lists birds heard during the night (lapwing, snipe, lark, tawny owl, and curlew) and 26 others at dawn. Actual times are given.

Smith, S. G. (1942). 'Response to colour in birds.' Nature, Lond. 150: 376–7.

Plasticine faeces (white, yellow, green, red and purple in order of brightness) were placed on the rim of a nest in the place from which they are normally removed by the adult in nest sanitation. First to be removed by meadow pipits were the green pellets, while a male yellow wagtail first removed the yellow ones. There was thus no correlation with brightness.

Beirne, B. P. (1942). 'Notes from Ireland.' Ent. Rec. 54: 131.

Short discussion of species of insects occurring in Ireland, but feeding on non-native plants.

Parmenter, L. (1942). 'Dolichopodidae (Dipt.) associated with flowers.' Ent. Mon. Mag. 78: 252.

Insect visitors to hogweed, sea carrot, tormentil and lesser stitchwort.

Edelsten, H. M. (1942). '*Pachyprotasis variegata* Fallén (Hym., Tenthredinidae) on potato.' Ent. Mon. Mag. 78: 292.

This sawfly has not previously been recorded as a pest of potatoes in Britain.

Gunn, D. L. & Walshie, B. M. (1942). 'The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. IV. Temperature preference.' J. Exp. Biol. 19: 133–41.

Aggregations occurred in a temperature gradient apparatus at 4 and 24° C. The latter is favourable for growth and other activities. The animals at 4° C. were 'metabolically trapped' through becoming immobilized in this cold zone.

Harrison, G. Heslop (1942). 'Notes on the genus *Psyllopsis* Löw (Hem., Psyllidae) with special reference to the British species found on *Fraxinus*.' Ent. Mon. Mag. 78: 155–60.

Some of these jumping plant-lice are gall-makers, other species of insects are often found within the galls.

Beirne, B. P. (1942). 'Notes on some Lepidopterous pests on fruit trees, and their parasites, in Ireland during 1941.' Econ. Proc. R. Dublin Soc. 3: 107–18.

Notes on collections from apple, pear, currant, raspberry and loganberry.

Praed, C. W. Mackworth- (1942). '*Carterocephalus palaemon* in Western Inverness-shire.' Entomologist, 75: 216.

This very local East Midland butterfly, the chequered skipper, is represented by a pale and sharply marked form in a hitherto unsuspected Scottish locality. One of the most astonishing discoveries about British butterflies this century.

Clark, E. J. (1942). 'Occurrence of *Chorthippus parallelus* (Zett.) f. *macroptera* (Orth., Acrididae) in Britain.' Ent. Mon. Mag. 78: 161–6.

Previous to this paper only two published records of the occurrence in Britain of the macropterous form of this common grasshopper were known. In 1941 the long-winged form occurred in seven out of sixteen colonies studied in Berkshire, Buckinghamshire and Surrey, a total of 8 males and 22 females out of 460 males and 411 females examined. It is concluded that environmental factors, more especially general seasonal effects are mainly responsible.

Brown, E. S. (1942). 'Two macropterous specimens of *Chorthippus parallelus* Zett. (Orthoptera).' Ent. Mon. Mag. 78: 167.

A macropterous male of this grasshopper found in Gloucestershire and another in Oxfordshire.

Browning, H. C. (1942). 'The relation of instar length to the external and internal environment in *Tegenaria atrica* (Arachnida).' Proc. Zool. Soc. Lond. A, 111: 303–17.

Instar length was found to vary with both kinds of factor. Increase of temperature, presence of illumination and fall in saturation deficiency all decreased instar length. Offspring of various parents fell into three groups according to mean instar length.

Kalmus, H. (1942). 'Anemotaxis in soft-skinned animals.' Nature, Lond. 150: 524.

Slugs (*Agriolimax reticulatus, Arion subfuscus, Arion hortensis*), snails (*Helix hortensis, Helix aspersa*), earthworms, and maggots of *Calliphora* and *Drosophila*, in experiments, turned and faced away from the wind. A very gentle air current only caused the head to turn towards the wind.

Dainton, B. H. (1942). 'Effect of air currents, light, humidity and temperature on slugs.' Nature, Lond. 151: 25.

Slugs (*Agriolimax reticulatus* and *Limax maximus*) placed in an air current, eventually moved away from it, through influence of the air on the tentacles. A current directed on the tail speeded up movement. The results were similar in saturated and unsaturated air, showing that they were not due to cooling on evaporation. Strong light caused temporarily increased activity. Reaction in avoiding drafts took priority over the reaction of not moving from dim to bright light. Activity was unaffected by changes in humidity. Changes in temperature caused marked changes in activity, but constant temperatures eventually produced the same activity, at any rate within certain limits.

Stephenson, W. (1942). 'The effect of variations in osmotic pressure upon a free-living soil nematode.' Parasitology, 34: 253–65.

Continues the account of experimental work on *Rhabditis terrestris*. The cuticle does not act as an impermeable outer covering. In both hypo- and hypertonic environments the main aqueous exchanges take place through the cuticle and are controlled by the underlying protoplasm. The species normally lives in a hypotonic environment and shows more efficient osmotic regulation in a hypotonic medium and even in distilled water.

(*d*) Small islands

Walton, G. A. (1942). 'The aquatic Hemiptera of the Hebrides.' Trans. R. Ent. Soc. Lond. 92: 417–52.

A comprehensive account.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Reid, J. A. (1942). 'On the classification of the larvae of the Vespidae (Hymenoptera).' Trans. R. Ent. Soc. Lond. 92: 285–331.

Descriptions and keys. The larvae of the four subfamilies, Eumeninae, Vespinae, Polistinae and Polybiinae, can be clearly distinguished from one another. It appears, however, that it is less difficult to distinguish the species than the genera.

Van Emden, F. I. (1942). 'Larvae of British beetles. III. Keys to the families.' Ent. Mon. Mag. 78: 206–26; 253–72.

Contains one key based on superficial characters and another attempting to classify the larvae.

China, W. E. (1942). 'A revision of the British species of *Cixius* Latr. (Homoptera), including the description of a new species from Scotland.' Trans. Soc. Brit. Ent. 8: 79–110.

Ten British species of this bug are now recognized in Britain. The nymphs are apparently all root feeders and live in crevices of the soil surrounded by waxy filaments.

Ledingham, I. C. & Wells, G. P. (1942). 'Narcotic for marine invertebrates.' Nature, Lond. 150: 121–2.

In magnesium chloride (80 g. per litre of tap water) soft bodied marine animals become relaxed and expanded in 1–4 hr., can then be killed with formalin and preserved as desired.

3. PARASITES

O'Mahony, E. (1942). 'Notes on Irish Siphonaptera: V.' Ent. Mon. Mag. 78: 199.

Records of eight fleas and their hosts.

Donisthorpe, H. (1942). 'British insects infested with Laboulbeniaceae.' Entomologist, 75: 175–8.

The hosts of these ectoparasitic fungi are mainly Carabid and Staphylinid beetles.

Donisthorpe, H. (1942). 'Laboulbeniaceae and ants.' Ent. Mon. Mag. 78: 193–9.

An account of ectoparasitic fungi found on the bodies of living insects.

Parkin, E. A. (1942). 'Symbiosis and Siricid woodwasps.' Ann. Appl. Biol. 29: 268–74.

The fungus, *Stereum sanguinolentum*, is present in the intersegmental sacs situated at the anterior end of the ovipositor of adult female *Sirex gigas* and *S. cyaneus*. The egg becomes infected with fungal oidia at the start of its passage down the ovipositor. Fungal growth begins immediately the egg is deposited and precedes the larva which is probably partly mycetophagous. The integument of a proportion of the larvae, possibly the females only, is modified into hypopleural organs which contain the fungus.

Hamm, A. H. (1942). 'Breeding notes on *Agria mamillata* Pand. (Dipt., Tachinidae).' Ent. Mon. Mag. 78: 234–5.

This fly is a parasite of the pupa of the moth *Yponomeuta cognatella* the gregarious larvae of which are such a pest on *Euonymus japonicus* used as a boundary to city gardens.

Hamm, A. H. (1942). 'Records of bred Tachinidae (Dipt.) chiefly from the Oxford district.' Ent. Mon. Mag. 78: 191–2.

A list of parasitic flies and their hosts, mainly butterflies and moths.

Audcent, H. (1942). 'A preliminary list of the hosts of some British Tachinidae (Dipt.).' Trans. Soc. Brit. Ent. 8: 1–42.

Includes a list of parasites with their hosts, a list of hosts with their parasites, and a list of sources of records.

Kerrich, G. J. (1942). 'Second review of literature concerning British Ichneumonidae (Hym.), with notes on Palaearctic species.' Trans. Soc. Brit. Ent. 8: 43–77.

Includes survey of taxonomic literature, British local lists, notes on Mr L. A. Carr's Ichneumonidae collections, notes on species, summary of host-parasite records, and references.

Vevai, E. J. (1942). 'On the bionomics of *Aphidius matricariae* Hal., a Braconid parasite of *Myzus persicae* Sulz.' Parasitology, 34: 141–51.

This study is interesting since the aphid *M. persicae* is a highly efficient vector of potato viruses, leaf roll, etc. *A. matricariae* is an internal parasite the larvae of which feed on the embryos of the host and later on the gut and other internal organs, preventing reproduction. Chronology of development given at various temperatures also rate of infestation under controlled conditions.

Beirne, B. P. (1942). 'Observations on the life-history of *Praon volucre* Haliday (Hym. Braconidae), a parasite of the mealy plum aphis (*Hyalopterus arundinis* Fab.).' Proc. R. Ent. Soc. Lond. A, 17: 42–7.

Rees, G. (1942). 'The worm burden of sheep on improved and unimproved hill pastures.' J. Anim. Ecol. 11: 198–204.

Although the sheep from both pastures, wintered together on a poor lowland pasture, where infestation occurs, the egg count of those on unimproved is higher than that of those on improved pasture.

Stephenson, W. (1942). 'On the culture of *Rhabditis terrestris* n.sp.' Parasitology, 34: 246–52.

A new species of nematode. It was cultured on a medium of 2 parts 0·6 % agar solution to 1 part earthworm broth. The following effects were noted to arise from increasing this food supply: (1) growth, apparent as increase in body length and thickness and particularly in length of intestine, (2) increased longevity, (3) increase in number of eggs laid by an individual and the production of more male larvae. The mean dimensions of the parts of females raised in different types of culture are given, and emphasize the inadequacy of specific descriptions based on single measurements without reference to environmental variation.

MacLeod, J. & Craufurd-Benson, H. J. (1941). 'Casual beds as a source of louse infestation.' Parasitology, 33: 211–13.

80 % of inmates of a common lodging house were lousy; 32·2 % of beds occupied more than four nights were also lousy.

4. FOOD AND FOOD HABITS

B——, K. B. (1942). 'Food of the grey lag goose.' Vasculum, 27: 22–3.

A stomach of a specimen shot near the Estuary of the Tay contained tubers the size of a hazel nut; two of the least digested ones began to grow and produced leaves like those of the sea club-rush, *Scirpus maritimus*.

Carpenter, G. D. Hale (1942). 'The relative frequency of beak-marks on butterflies of different edibility to birds.' Proc. Zool. Soc. Lond. A, 111: 223–31.

Distasteful species are shown to be attacked and released more often than edible species.

Barclay, O. R. (1942). 'Feeding of the common toad.' Nature, Lond. 150: 376.

Some excellent photographs provide evidence against the theory that protrusion of the tongue is effected by lymph pressure. A muscular mechanism appears to be responsible. The entire movement occupies about $\frac{1}{10}$ sec.

Popham, E. J. (1942). 'The variation in the colour of certain species of *Arctocorisa* (Hempitera, Corixidae) and its significance.' Proc. Zool. Soc. Lond. A, 111: 135–72.

Counts taken in two parts of England (Surrey and Lancs) show that the body colour in *Arctocorisa distincta* is correlated with the tone of the background. This colour is not changeable. Experiments using rudd (*Leuciscus erythrophthalmus*) as predators showed that insects on a background of their own tone were less liable to be caught. Selection pressure decreased with increasing density of prey and with an increasing ratio of protected/unprotected in the population.

Wilson, G. Fox- (1942). 'The harvesting of alder buckthorn (*Rhamnus frangula*) and the effect on the insect fauna.' Proc. R. Ent. Soc. Lond. A, 17: 112.

An opportunity of studying the effect of the temporary disappearance of an essential food-plant upon the brimstone butterfly and *Aphis rhamni*.

Jones, M. G. (1942). 'The summer hosts of *Aphis fabae* Scop.' Bull. Ent. Res. 33: 161–9.

Field experiments showed the general order of preference was (1) bean (2) seed beet (3) dock, *Chenopodium* and poppy (4) thistle.

Parmenter, L. (1942). 'The prey of a population of *Machimus atricapillus* Fallen (Diptera).' Proc. R. Ent. Soc. Lond. A, 17: 71–2.

A list of the prey of 24 males and 17 females in one locality in Cornwall.

Harrison, J. W. Heslop (1942). 'The effect of larvae on the gall-gnat, *Contarinia steini* Karsch (Dipt., Cecidomyidae) on the flower colour of white-flowered *Lychnis dioica* L.' Ent. Mon. Mag. 78: 231.

Flowers infested with larvae of this fly were pink, possibly on account of enzyme action.

Harvey, H. W. (1942). 'Production of life in the sea.' Biol. Rev. 17: 221–46.

The productivity of a water mass is defined as the quantity of organic matter produced by the phytoplankton over a period of time such as a year. Indirect methods for estimating this productivity are described, e.g. from the decrease in nitrate, phosphate or carbon dioxide in a known body of water. The validity of such methods is discussed and their estimates compared over a period of years. Observations on certain interrelated factors which effect productivity are reviewed: (1) quantity of light energy available, which is related to the turbidity of the water, (2) turbulence, which, though often increasing turbidity, also carries up nutrient salts from lower levels, (3) rate of supply of nitrogen and phosphorus to the photosynthetic zone, (4) influence of factors such as light and salt concentration on growth rate in diatoms, (5) effects of grazing and excretions of herbivores on the breeding stock of plants, (6) effects of bacteria and enzymes in regenerating nutrient salts, (7) the supply of iron and other trace elements needed by certain diatom species and the effect of such supply on the density distribution of plant life in the South Atlantic.

Raymont, J. E. G. & Gross, F. (1942). 'On the feeding and breeding of *Calanus finmarchicus* under laboratory conditions.' Proc. Roy. Soc. Edinb. 61: 267–87.

Females survived much better than males and ate about forty times as much. Both large and very small phytoplankton were successfully utilized.

5. POPULATION STUDIES

Evans, F. C. (1942). 'Studies of a small mammal population in Bagley Wood, Berkshire.' J. Anim. Ecol. 11: 182–97.

From October 1936 through February 1939 trapping and marking were done on two grids covering a variety of habitats. The chief species were the wood-mouse (*Apodemus sylvaticus*) and bank-vole (*Clethrionomys glareolus*). About half the population disappeared within one month after first capture. Both species have fairly small home ranges. Distribution was not random. As population 'survival' from a period of high to low density appeared greater in habitats of low density, it is suggested that 'unfavourable' low density habitats may be essential to the ultimate survival of a species.

Brambell, F. W. Rogers (1942). 'Intra-uterine mortality of the wild rabbit, *Oryctolagus cuniculus* (L.).' Proc. Roy. Soc. B, 130: 462–79.

A large proportion of embryos was resorbed at all stages of gestation, but particularly about the 11th and 12th day. From a comparison with the number of corporea lutea it was found that 42–56% of all litters were lost before the 20th day. These data are for 185 pregnant rabbits from Caernarvonshire, February to July 1941.

Bullough, W. S. (1942). 'The reproductive cycles of the British and continental races of the starling (*Sturnus vulgaris* L.).' Phil. Trans. Roy. Soc. B, 231: 165–246.

Of the starlings found in Britain in autumn and winter those with small gonads are immigrants from the continent and roost communally. The resident starlings have more advanced sexual and secondary sexual characteristics and roost in holes. These conclusions are supported by records from ringing, and it is proposed that the resident bird be recognized as a physiological subspecies of the continental.

Southern, H. N. & Reeve, E. C. R. (1932). 'Quantitative studies in the geographical variation of birds.—The common guillemot (*Uria aalge* Pont.).' Proc. Zool. Soc. Lond. A, 111: 255–76.

The bridled variety of the common guillemot is distributed in an increasing ratio to the ordinary form from south to north and, to a less extent, from east to west of the range. The increase in percentage of bridled birds is not steady but occurs in steps, regions of fairly gradual change alternating with zones of rapid change. Statistical analysis of counts in which component ledges were kept separate, shows that, with one surprising exception, bridled birds were distributed at random throughout the populations.

McWilliam, J. M. (1942). 'The Scar Rocks Gannetry, 1942.' Brit. Birds, 36: 62–4.

First nests were reported here in 1939. The colony now numbers 20–25 pairs.

Venables, L. S. V. & Wykes, U. M. (1942). 'An index to the Thames kingfisher recovery.' Brit. Birds, 36: 153–5.

Counts of birds between Rushy Weir, Bampton, and Reading during 1940–42 show an increase of 3–24 in winter and from 2–15 in the breeding season, the original low number being due to severe conditions in the winter of 1939–40.

Worthington, E. B. (1942). 'The Windermere perch fishery and possibilities of its expansion.' Fish. Gaz. 3 Jan. 1942.

Includes a diagram of the 'lobster pot' type of trap whereby over a million undersized perch were removed from Windermere in May and June 1941 for canning.

Hardy, E. (1942). 'Salmon of the Welsh Dee: how the runs have changed.' Salm. Trout Mag. Lond. No. 106: 256–61.

A discursive account of the age, growth and migration of salmon in the Welsh Dee, recording that since the beginning of this century a spring run of fish has become established. It is suggested that this is due to the introduction of Scottish stock.

Proceedings of the Association of Applied Biologists (1942). 'Symposium on domestic entomology.' Ann. Appl. Biol. 29: 309–21.

Information on the quantitative aspects of scabies parasitology by **C. G. Johnson**; flies in town and country by **H. G. H. Kearns**; furniture beetles and other wood-borers by **R. C. Fisher**; and the invasion of houses by ants and ear-wigs by **G. Fox-Wilson.**

Massee, A. M. (1941). 'Notes on some interesting insects observed in 1940.' Rep. E. Malling Res. Sta. 1940: 61–5.

Account of occurrences and, in some cases, bionomics and control, of strawberry *Rhynchites* (*R. germanicus*), shot-hole borer (*Anisandrus dispar*), hop-strig maggot (*Contarinia humuli*), black-currant midge (*Dasyneura tetensi*), apple Capsid bug (*Plesiocoris rugicollis*), strawberry and *Rubus* aphides, hop froghopper (*Evacanthus interruptus*), apple leafhopper (*Typhlocyba frogatti*), plum leafhopper (*Eupteryx stellulata*), and cuckoo-spit (*Cereopis sanguinea*).

Proceedings of the Association of Applied Biologists (1942). 'Symposium on the pathology of the hop.' Ann. Appl. Biol. 29: 322–32.

Includes notes by A. M. Massee on the hop-damson aphis, the hop red spider, strig maggot, hop flea beetle and other important pests of the hop as well as a list of insects tested as possible vectors of mosaic and nettlehead.

Thompson, H. W. (1942). '*Crambus hortuellus* Hb. as a grassland pest.' Ann. Appl. Biol. 29: 393–8.

Infestation was as high as 128 caterpillars or cocoons per sq. ft. of turf on upland fields in which fescues and bent predominated. The effect of parasitism and the attacks of birds are briefly discussed.

Barnes, H. F. (1942). 'Unusual abundance of *Notolophus* (=*Orgyia*) *antiqua* L. (Lep., Lymantriidae).' Ent. Mon. Mag. 78: 240.

A rough assessment of the number of caterpillars of the vapourer moth gave a density of 1250 per square foot in a restricted area among bilberry in North Wales.

Petherbridge, F. R., Wright, D. W. & Davies, P. G. (1942). 'Investigations on the biology and control of the carrot fly (*Psila rosae* F.).' Ann. Appl. Biol. 29: 380–92.

Includes observations on the emergence and abundance in the field of the first and second generations of the fly. The flies feed on the flowers of wild chervil and hemlock, the latter being a host for the larvae of both generations. See also **Barnes (1942)** and **Baker, Ketteringham, Bray & White (1942).**

Gough, H. C. & Evans, A. C. (1942). 'Some notes on the biology of the click beetles *Agriotes obscurus* L. and *A. sputator* L.' Ann. Appl. Biol. 29: 275–9.

A. obscurus females laid significantly more eggs in grass and significantly fewer eggs in bare fallow than in clover, wheat and kale in a laboratory experiment. Marked adults of *A. sputator* were caught up to 30 yards away from their liberation point.

Le Pelley, R. H. (1942). 'A method of sampling thrips populations.' Bull. Ent. Res. 33: 147–8.

Wide mouthed 16 oz. bottles with screw caps are filled with 70% alcohol. The infested leaves are dipped in and then thrown away. The alcohol is filtered and the thrips counted under a low-power binocular microscope on filter paper ruled with lines a little less than 1 cm. apart. A formula is given of a solution for making a blue print of the filter paper for use with light coloured insects.

Mellanby, K. (1942). 'Natural population of the head-louse (*Pediculus humanis capitis*: Anoplura) on infected children in England.' Parasitology, 34: 180–4.

All live lice were collected by combing from 45 boys and 48 girls under 14 in a northern industrial city. Average number of lice per head was 12·7 for boys and 16·8 for girls. The presence in most cases of all stages of lice, and the position of the nits, made it evident that the infestation had been established for some time. Such long established light infestations are probably kept down by combing and may thus act as a persistent source in infestation.

Lucas, D. E. (1942). 'Continuous plankton records: phytoplankton in the North Sea, 1938–39. Part II. Dinoflagellates, Phaeocystis, etc.' Hull Bull. Mar. Ecol. 2: 47–70.

From monthly transects it was found that there was a long term fluctuation in density of Dinoflagellates. From a decrease in the southern area in 1933 numbers built up until 1938. During 1939 there was a colossal reduction in numbers, particularly on the Hull-Bremen line.

Lucas, C. E., Marshall, N. B. & Rees, C. B. (1942). 'Continuous plankton records: the Faroe-Shetland channel, 1939.' Hull Bull. Mar. Ecol. 2: 71–94.

The spring crop of phytoplankton first appeared over the Faeroe Bank and near the Orkneys. After this diatoms increased up to July and August, being densest in the channel between these two areas. Although the channel was thus more productive than the bank, diatoms were scarce in the deep water beyond it.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Bullough, W. S. (1942). 'The starling (*Sturnus vulgaris* L.) and foot-and-mouth disease.' Proc. Roy. Soc. Ser. B, 131: 1–13.

The average number of starlings occupying communal roosts is high in autumn and winter, low in spring and summer when the continental starlings have left Britain. Incidence of unexplained outbreaks of foot-and-mouth disease corresponds closely in time with these changes. In Sweden outbreaks are highest in spring: and this is the time the starlings return. The migration routes from Sweden, Denmark and the Baltic are further circumstantial evidence that there may be mechanical carriage of the disease.

Gordon, S. (1942). 'The fulmar in the British Isles.' Nature, Lond. 150: 313–14.

Comments on the paper by **Fisher & Waterston** (1941, J. Anim. Ecol. 10: 204–72) suggests that part of the eastward spread of the fulmar was through following whales being towed from St Kilda to Harris. Probably the arctic fox and great black-backed gulls prey on fulmars. The St Kildans used to fence off the fulmar cliffs to prevent sheep disturbing the birds.

Parmenter, L. (1942). '*Chrysotus pallidipalpus* Van Duzee (=*elegans* Parent) (Dipt., Dolichopodidae) in Britain.' Ent. Mon. Mag. 78: 232–3.

This fly was originally described from Honolulu. It has several times been found in British hot-houses.

Richards, O. W. (1942). '*Graphocephala coccinea* (Forst.) (Homopt., Cicadellidae) in Buckinghamshire.' Ent. Mon. Mag. 78: 252.

This American bug first recorded from Surrey in 1935 has now twice been taken near Slough.

Crowson, R. A. (1942). '*Leistus rufomarginatus* Duft. (Col., Carabidae) new to Britain.' Ent. Mon. Mag. 78: 281–2.

This conspicuous European ground beetle has now been found under dead leaves near Sevenoaks and may have been introduced from Holland.

7. REPORTS OF ORGANIZATIONS

Freshwater Biological Association of the British Empire. Tenth Annual Report for the year ending 31st March, 1942. 37 pp. Price to non-members 1*s.* 6*d.*

The war has led to some modification of the programme of the Wray Castle laboratory; but though hydrology, bacteriology and algology have had to receive less attention, the report shows that work on fish and fisheries (perch, eels, minnows, char and trout) has been continued on the fullest possible scale with particular reference to economic problems.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1942

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance:		
Members taking *Journal of Ecology* only	241 7 3	
Members taking *Journal of Animal Ecology* only ...	124 5 0	
Members taking both Journals	110 0 9	
Associates	1 2 6	
		476 15 6
Interest on Investments	52 0 0	
Interest on Deposit Account	1 19 11	
		53 19 11
Journal of Ecology:		
Sales—less Expenses		4 7 7
Index vols. I–XX, Sales—less Expenses		1 7 6
Grant from Royal Society		150 0 0
		£686 10 6
Journal of Ecology, 1942:		
Sales: Current vol. 30	427 13 6	
Back volumes and parts	134 4 0	
Reprints	18 6 0	
		580 3 6
Grant for Illustrations, Balliol College, Oxford ...		8 0 0
Grant from Burtt-Swynnerton, Memorial Appeal Fund, towards Special Supplement		150 0 0
		£738 3 6
Journal of Animal Ecology, 1942:		
Sales: Current vol. 11	203 19 0	
Back volumes and parts	53 6 3	
Reprints	64 5 6	
		321 10 9
Balance (see above, under Expenditure)		278 14 0
		£600 4 9
Biological Flora of the British Isles, 1942:		
Sales of Reprints of Articles		11 5 2
Balance (see above, under Expenditure)		34 10 3
		£45 15 5

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing and Stationery	3 4 3	
Postages	8 2 1	
Travelling	12 19 5	
Exps: re Biology War Committee	10 14 10	
Exps: re Committee on Nature Reserves	4 0 11	
Expenses of Meetings	1 11 6	
Audit Fee	3 3 0	
Sundries, typing, etc.	8 10	
Clerical assistance	12 0 0	
		56 4 10
Grant: to Freshwater Biological Association		10 0 0
Biological Flora of the British Isles. Cost of Printing, *less* Sales		34 10 3
Journal of Animal Ecology. Cost *less* Sales		278 14 0
		379 9 1
To Balance, Surplus for Year, carried forward ...		307 1 5
		£686 10 6
Journal of Ecology, 1942:		
Costs: Paper, Blocks, Printing and Binding ...	627 2 0	
Publishers' Commission	80 5 9	
Carriage and Postages	20 7 7	
Insurance of Stock	5 6 1	
Advertising, etc.	14 6	
		733 15 11
Balance (see above, under Income)		4 7 7
		£738 3 6
Journal of Animal Ecology, 1942:		
Costs: Paper, Blocks, Printing		524 14 11
Checking Literature References		10 0 0
Publishers' Commission		42 10 6
Carriage, etc.		12 2 6
Insurance of Stock		10 2 10
Advertising		14 0
		£600 4 9
Biological Flora of the British Isles, 1942:		
Costs: Printing Reprints of Articles, etc.		43 10 0
Publishers' Commission		1 2 6
Carriage, etc.		1 2 11
		£45 15 5

BALANCE SHEET AT 31 DECEMBER 1942

Assets

	£ s. d.	£ s. d.
Cash at Bank, Current Account	239 2 9	
" " Deposit Account	400 0 0	
		639 2 9
Publishing Accounts—Amounts due from Cambridge University Press:		
Journal of Ecology. Balance of Account	273 3 6	
" " Index Volume	1 7 6	
Journal of Animal Ecology. Balance of Account ...	140 1 11	
Biological Flora of the British Isles...	8 19 9	
		423 12 8
Investments at Cost		1,428 14 1
		£2,491 9 6

Notes *re* Investments:

	£ s. d.
Cost: £200 of 5% Conversion Loan...	198 10 0
£1,050 of 3½% War Loan ...	1,070 6 10
£150 of 3½% War Loan bought March 1942	159 17 3
	£1,428 14 1

Market Value of the above Investments:

£1,200 of 3½% War Loan at 105½ ...	1,266 0 0
£200 of 5% Conversion Loan at 102 ...	204 0 0
	£1,470 0 0

A further Asset, not valued, is the Unsold Stock of Journals, and Index Volume held by the Publishers for the Society.

VICTOR S. SUMMERHAYES,
ALEX. S. WATT.
Hon. Treasurers.

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1943/44... ...		10 15 0
Library Fund		1 5 0
Balance of Printing Accounts due:		
Journal of Ecology, vol. 30, no. 2 and Reprints ...	222 15 1	
Journal of Animal Ecology, vol. 11, no. 2 and Reprints	259 13 2	
Biological Flora of the British Isles	20 2 9	
		502 11 0
Sundry Accounts due:		
Arliss, for Stationery	1 14 0	
Cambridge University Typewriting Office	4 0 11	
		5 14 11
General Revenue Account:		
Surplus in hand 31 December 1941	1,664 2 2	
Surplus for year ending 31 December 1942 ...	307 1 5	
		1,971 3 7
		£2,491 9 6

Audited and found correct and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants.

120 BISHOPSGATE, E.C. 2
and
231*a* HIGH ROAD, LOUGHTON, ESSEX.
3 *April* 1943.